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Announcement

The American Society of Limnology and Oceanography has established LIMNOLOGY AND OCEANOGRAPHY in response to a need felt by its members for a common outlet for the publication of scientific papers on all aspects—physical, chemical, geological and biological—of the phenomena exhibited by natural bodies of water.

The Society was organized in St. Louis on January 1, 1936, as the Limnological Society of America. It had become apparent at that time that interest in freshwater biology and the physical factors which control the fresh water environment had grown to a point where a separate organization was needed to encourage scientific work in this aspect of ecology. Just as it had been accepted from the start that students of the biological, chemical and physical aspects of limnology had much to gain by association, so it was soon realized that the differences between fresh and salt water systems were trivial, when compared to the common principles with which limnologists and oceanographers alike are concerned. In 1948 the organization was renamed the American Society of Limnology and Oceanography and physical oceanographers and marine biologists assumed their share in the privileges and responsibilities of membership.

Limnology and Oceanography is offered now to all those concerned with aquatic science, both in this country and abroad, in the faith that it will serve a useful purpose by providing a common medium for technical papers on the varied specialties which unite to increase our understanding of the aquatic environment.

Alfred C. Redfield, *President*
American Society of Limnology and Oceanography

Environmental Factors Affecting Growth in *Venus mercenaria*[1]

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ABSTRACT

The results of a five years' study of variations in quahog growth rates in Narragansett Bay are summarized. Linear increments are inversely proportional to initial length over the size range 35–70 mm (greatest dimension), whereas volumetric increments in this range are approximately constant. Growth in some parts of the Bay is three times as fast as in others. Most of the year's growth occurs before mid-July, and growth rates showed no significant variation from year to year. Annual increments in Narragansett Bay are considerably greater than at Prince Edward Island, and they appear to fall in the same general range as those reported for New Jersey and the south side of Cape Cod.

The effects of various environmental factors on growth have been investigated over a three-year period. Growth was not appreciably influenced by existing differences in current speed, dissolved oxygen content, or salinity of the bottom water. Temperature imposes an upper limit to the potential rate of growth, which is negligible below 10°C and rises with increasing temperature at least to 23°C. Comparisons of growth rates with phytoplankton concentrations suggest that small diatoms, either living or as detritus, are an important source of quahog nutrition in these waters. Growth is retarded in sediments with a high silt-clay content. This effect is discussed in relation to the concomitant reduction in sediment permeability, the possible accumulation of inhibitory substances, and the necessity for more frequent clearing of the animals' filtering apparatus.

A dredging survey of Narragansett Bay, a 100-square mile estuary in Rhode Island, has shown that the quahog, *Venus mercenaria* Linnaeus, is the most abundant animal of its size living in or on the bottom, and constitutes a significant fraction of the total bottom dwelling community (Pratt 1953). Growth studies *in situ* have been made over a period of five years. These have secondarily produced a volume of data on local variations in quahog growth rates, but the primary objective of the study has been to identify and measure quantitatively the principal environmental factors governing the growth of this widespread, abundant, and commercially important bivalve. Information concerning these factors would apply wherever the species occurs, and might contribute to a fuller understanding of growth in related forms. For a review of recent ecological studies of marine molluscs, the reader is referred to Turner (1953b).

[1] Contribution No. 13 from the Narragansett Marine Laboratory. These studies were aided by contract NR 163-100 between the Office of Naval Research, Department of the Navy, and the University of Rhode Island.

Two problems have received special attention:

(1) The sources of nutrition of the Pelecypoda are not precisely known. Before the flagellates were recognized as an important potential food of filter feeders, it was generally assumed but never demonstrated that clams, oysters, mussels, etc., depended primarily on living plankton diatoms. Studies of stomach contents in these relatively indiscriminate filter feeders have not shown what substances ingested actually contribute to growth, nor has the success of various investigators in rearing oyster larvae on cultures of diverse microorganisms advanced our knowledge of the sources of nutrition of adult bivalves in a natural state. Turner (1953a) has obtained fairly rapid growth in quahogs in outdoor tanks with a high concentration of phytoplankton maintained by inorganic fertilizers, and he reports (Turner 1953b) that H. H. Haskin has shown good agreement between the rate of quahog growth and the amount of food of an unspecified nature, as indicated by the total phosphate and chlorophyll content of the overlying

waters. Coe (1948) has stressed the importance of organic detritus in the nutrition of certain West Coast bivalves, basing his conclusions on field and laboratory observations and a number of assumptions. Current opinions agree in one point only: that the majority of pelecypods subsist largely on particulate matter in suspension. The relative importance of detritus and of the various elements of living plankton in the nutrition of bivalve molluscs (including the much-studied oyster) is as yet unknown.

(2) The growth of marine pelecypods is not controlled exclusively by properties of the water. Recent work has shown that *Mya arenaria* (Swan 1952) and *Venus mercenaria* (Pratt 1953) grow faster in sand than in mud when other variables are eliminated. The sediment factor or factors responsible for this effect and their modes of operation are not understood.

METHODS

Measurement of Growth

During the years 1950–1954 inclusive, oaken boxes filled with sediment and containing quahogs of different sizes were placed on the bottom at various points in the Bay in order to observe growth rates under different combinations of environmental conditions. The boxes were 2′ x 2′ x 1′ deep, with numerous holes bored through the bottom to allow communication between the box sediment and that beneath. Each was marked with a surface buoy. The localities selected (Fig. 1) varied somewhat from year to year and covered as wide a range of ecological conditions as was compatible with the limitations imposed by boat traffic, the operations of scallop draggers, and strong tidal currents and wind-generated waves that tended to scour the sediment out of the boxes. Growth measurements were obtained during the years and at the stations shown in Table 1. (Boxes were also placed at eight other localities, not listed, but without results, owing to accidental loss, upsetting, or scouring of the box.) The letter "L" means that the box was filled with the local sediment; other letters refer to boxes filled with other natural sediments. The majority of the sediments were analyzed for particle size distribution, with the results given in Table 2.

FIG. 1. Narragansett Bay, showing station locations.

TABLE 1. *Experimental growth boxes, by station and year*

Station	Water Depth, Feet	1950	1951	1952	1953	1954
1	16	1L	1L			
2	9	2L	2L	2L, A	2L, A	
3	10		3L	3L		
4	14	4L	4L			
5	18	5L	5L			
6	4		6L	6L, B	6L, A	C, D, E
7	14	7L	7L	7L	7L, A	
8	16	8L				
9	14	9L	9L	9L	9L, A	C, D, E
10	9			10L	10L, A	

L = local sediment. A, B, C, D and E refer to other natural sediments.

As shown by Belding (1931) and Kerswill (1941) and by our own unpublished data, quahog growth is negligible at temperatures below 10°C. Practically speaking, this limits the growth season in Narragansett Bay generally to the months May–October,

TABLE 2. *Particle size distributions of sediments used in growth boxes and aquaria, by per cent weight*

Wentworth Scale	Size in mm	Sediments 1952							
		2L	A	3L	6L	B	7L	9L	10L
Pebbles	64–4	6.5	3.1	1.1	18.2	9.1	2.6	4.4	34.6
Granules	4–2	3.8	0.5	0.7	4.0	5.2	0.8	1.1	6.2
Very coarse sand	2–1	2.3	1.3	0.5	3.0	8.5	1.0	1.4	3.7
Coarse sand	1–½	4.2	4.2	0.6	2.8	17.3	4.4	2.8	3.8
Medium sand	½–¼	6.0	14.8	2.1	4.9	24.1	16.3	8.0	7.3
Fine sand	¼–⅛	10.4	43.9	30.8	4.5	6.7	46.9	27.1	10.2
Very fine sand	⅛–1/16	12.5	27.7	39.6	2.3	3.3	22.2	31.9	12.4
Silt and/or clay	<1/16	54.4	4.5	23.5	59.2	25.8	5.9	23.3	21.9

Wentworth Scale	Size in mm	Sediments 1953						Sediments 1954			
		2L	A	6L	7L	9L	10L	C "coarse sand"	D "fine sand"	E "mud"	Aquarium "mud"
Pebbles	64–4	6.2	3.1	2.6	2.6	4.4	38.0	13.0	—	1.2	0.1
Granules	4–2	1.8	0.5	1.4	0.8	1.1	6.0	13.1	—	0.7	0.1
Very coarse sand	2–1	3.4	1.3	1.8	1.0	1.4	4.5	25.9	—	1.6	0.4
Coarse sand	1–½	4.3	4.2	3.1	4.4	2.8	4.8	35.6	—	3.5	0.9
Medium sand	½–¼	5.4	14.8	5.5	16.3	8.0	9.4	10.6	0.5	11.9	6.8
Fine sand	¼–⅛	12.1	43.9	10.5	46.9	27.1	11.2	0.7	35.3	27.5	20.6
Very fine sand	⅛–1/16	23.2	27.7	11.5	22.2	31.9	10.3	0.2	55.3	22.6	29.4
Silt and/or clay	<1/16	43.5	4.5	63.7	5.9	23.3	15.8	0.9	9.0	28.8	41.8

NOTE: No sample was obtained of sediment 7L in 1952; in its place in the table, the analysis for 7L 1953 is given. Likewise the analysis of 9L 1952 is repeated for 9L 1953, of which no sample could be obtained. Analyses of Sediment A varied slightly from box to box and have been averaged.

inclusive. In 1950 the boxes were in place from late June to November, in 1951 from May 1 to November, and in 1952 from mid-June to November. In subsequent years the boxes were raised at regular intervals during the year to determine growth in a number of "growth periods", in order to provide more data for comparison with environmental factors. In 1953 the boxes were planted during the week of April 27 and raised for remeasurement every sixth week for a total of four growth periods, ending in mid-October. The 1954 season, from May 24 to November 7, was divided into three growth periods of eight weeks each. Earlier work (Pratt 1953) had shown that temporary removal of the animals from the sediment for measurement does not appreciably retard their growth. The 1951 and 1953 data represent the entire year's growth, whereas in the other years observations were not begun until after the start of the growing season.

The quahogs, all locally dug, were made individually identifiable by numbering their shells with ordinary enamel paint. The size of each animal was determined by measurement of shell length with a simple adaptation of the standard fish measuring board. Numbers of quahogs per box and the initial size ranges varied as follows: 1950, 80 animals of 30–70 mm in length; 1951, 80 of 35 or 40–70 mm; 1952, 120 of 25–55 mm; 1953, 100 of 30–55 mm; 1954, 100 of 35–45 mm. Growth was measured by noting the increase in shell length. However, the length increment does not give a true index of the actual increase in size, since, for example, as Belding (1931) has shown, a 5 mm increment for a quahog 25 mm long means a volume increase of only 2.17 ml, whereas for an animal 70 mm long the same linear increment means an increase of 13.40 ml. Hence linear increments have been converted to volumetric units by the use of a table prepared by Belding (1931), and growth rates are given in terms of milliliters. To facilitate comparison with growth data from other areas, increments are occasionally also expressed in the more

conventional form, namely in millimeters of length.

Measurement of Environmental Factors

During the first two years of growth measurement (1950, 1951) a lack of funds prevented the routine observation of ecological conditions. The award of an Office of Naval Research contract made possible, for 1952, 1953, and 1954, a program of weekly measurement of environmental factors believed to influence quahog growth rates, as listed below. The measurements were made of the bottom water at the growth sites.

Temperature was measured by reversing thermometer.

Current speeds were estimated by Price-Gurley current meter.

Salinity was determined by silver nitrate titration.

Dissolved oxygen was measured by the Winkler method.

Phytoplankton was estimated by counts made on fresh samples in a Sedgewick-Rafter counting chamber. In 1952 the samples were centrifuged for five minutes at 2400 rpm before counting. Subsequently, comparative counts of phytoplankton in raw fresh samples and centrifuged fresh samples showed that the centrifuge does not concentrate the living organisms effectively, with the result that the estimate of cell numbers per liter thus derived is erroneously low. Fortunately the plankton was generally so abundant that reasonably accurate counts could be made on one-milliliter aliquots of raw water in the Sedgewick-Rafter chamber, and this procedure was adopted for the 1953 and 1954 work. All cells were referred to one or another of four arbitrary size groups, viz., <15, 15–37, 38–75, and >75 μ in greatest dimension.

Samples of "bottom water" (actually taken about one foot above the bottom) were obtained with a one-gallon bottle, designed by Captain Stanley Spink, which opened automatically on contact with the bottom and closed when raised free.

Particle size distribution of the sediment was determined by use of Tyler sieves, Wentworth $\sqrt{2}$ scale (Krumbein and Pettijohn 1938: 137). Sediment pH and permeability were measured by methods described in the results under the heading "sediment type".

Because of the potential importance of suspended organic detritus in the nutrition of pelecypods and in the lack of any method of measuring this material directly, it seemed desirable to make some measurement that would at least include suspended detritus. Attempts to do this by micro-Kjeldahl determination of the particulate nitrogen in bottom water samples were, however, unsuccessful, and the results are omitted from the discussion.

Field work was conducted with the draggers BILLIE and LIL-JOY, operated by Captains Stanley T. Spink, George A. Spink, and R. E. Sutcliffe. We are also indebted to James E. Masterson, Clarence R. Munroe, and Theodore J. Smayda, summer assistants.

VARIATIONS IN GROWTH RATES

While the central aim of this study was to measure the more important environmental factors influencing the rate of quahog growth, observed differences in growth rates as to season, year, size and locality are briefly summarized for the sake of regional comparisons.

Growth relative to initial size. Information relating growth rate to size is available for quahogs ranging from 35 to 70 mm in length. Nine sets of data covering this range (from the 1950 and 1951 series) show that if growth is expressed in terms of length, the rate was inversely proportional to initial size, and on the average, animals 35–39 mm long grew 2.96 times as fast as animals 65–69 mm long. If, however, the increase is expressed in volumetric terms, the increment was nearly constant over the range examined, animals of 35–39 mm growing, on the average, only 1.16 times as fast as those of 65–69 mm.

Local variation. As a basis for comparing growth rates in the native sediments of different parts of Narragansett Bay, the size range 40–49 mm (initial length) pro-

TABLE 3. *Average growth increments in local sediments for quahogs of initial length 40–49 mm*

Stations	1950 (Late June to November)		1951 (May 1 to November)		1952 (Mid-June to November)		1953 (May 1 to November)	
	mm	*ml*	*mm*	*ml*	*mm*	*ml*	*mm*	*ml*
1	7.6	8.9	8.1	9.8				
2	6.8	8.2			6.0	8.0	8.9	10.6
3			8.6	10.7	9.3	10.9		
4	6.5	7.1	7.0	8.6				
5	5.2	5.6	8.8	11.1				
6			11.7	15.6	5.5	5.8	12.5	15.9
7	9.8	11.5	9.0	11.4	7.7	9.2	8.6	10.4
8	8.4	10.1						
9	5.2	5.8			5.5	6.0	7.3*	8.4*
10					5.1	5.7	4.6	6.4

* May 1 to September 10.

vides the largest available series of data, which are presented in Table 3. Each pair of values represents the mean growth of 11 to 55 animals, with an average of 30. In any one year, growth rates varied considerably from place to place, reflecting much of the total range of environmental conditions to be found in the Bay. The greatest differences observed between stations within a given year were nearly threefold.

Since the quahog is an estuarine animal and its centers of abundance in Narragansett Bay are in the inner reaches, one might expect lower growth rates in the seaward areas. This is confirmed in the consistently slow growth at Stations 9 and 10 nearest the mouth of the Bay (Fig. 1), although growth at certain other stations does not bear out the prediction; for example, growth rates were unexpectedly and consistently high at Station 7 (also high at 8), and unaccountably low at Station 4. If adequate data were available, such differences could doubtless be explained on the basis of local conditions, since the complex configuration of the Bay probably results in a high degree of local variation rather than a continuous gradient of environmental factors from the head to the mouth of the Bay.

The different stations usually ranked consistently from year to year in their relative growth rates, so that in most cases growth at a given station could be roughly estimated from growth at others. A marked exception to this is seen in Station 6, which is unique in its extremely estuarine character. The pronounced fluctuations in annual growth at this locality probably reflect an environmental complex far less stable than that of the open Bay. Station 5, however, showed a similar discrepancy in annual growth (compare 1950 and 1951, Table 3), which apparently cannot be explained on the same basis and is not understood.

Annual variation. The available information concerning yearly differences in growth are again those given in Table 3. Growth increments averaged somewhat greater in 1951 and 1953 than in 1950 and 1952, but this difference is explained by the fact that observations were not begun until June in the last-mentioned years. It is therefore concluded that over the period 1950–53, except for Stations 5 and 6 as noted above, growth rates for the Bay as a whole showed no significant annual variation.

Seasonal variation. The relative importance of different parts of the growing season varied with locality, but in nearly every case in which a full year's growth was recorded, more than one-half of the annual growth occurred before mid-July. This finding agrees with the results of a previous study of growth rates in Wickford Harbor, near the present Station 6 (Pratt 1953).

Comparison with other areas. Mean annual growth increments in Narragansett Bay are compared in Figure 2 with growth at other points on the Atlantic seaboard. The Prince Edward Island increments are taken from Kerswill (1941), who measured the annual growth of quahogs 33–34 mm long in experimental plots in the Bideford River. His data, originally expressed as increase in the dorso-ventral axis, are given here in terms of length (antero-posterior axis), by use of a factor supplied by Kerswill. He obtained length increments averaging 8.4 mm for one year, and 5.9 mm for another. The curve for the western shore of Cape May, N. J., which has been derived from a figure (Haskin 1954) showing annual weight increments, by applying Haskin's formula relating weight to length, cannot be regarded as more than an approxima-

tion. The Cape Cod data are taken directly from Belding (1931).

According to Figure 2 annual growth is greater at Monomoy Point on the south side of Cape Cod than at the other localities from which information is available. Belding's data, however, are perhaps not representative of the Cape Cod area, since he describes Monomoy Point as "a favorable place for growth" and states that "in some localities the growth was only one-fourth as rapid". The Cape May increments are close to a four-year average for that particular area, which showed the highest growth rates of six localities in New Jersey studied by Haskin. The curve for Narragansett Bay, by comparison, is believed to approximate an average for the Bay populations; the points plotted are the mean increments for Stations 1, 2, 3, and 4 in 1951 and Stations 2, 6, 7, and 10 in 1953. These differences make comparisons between the four areas difficult. Possibly more extensive data would show that average annual growth increments differ but little from New Jersey to the south side of Cape Cod. In the cooler waters and shorter season at Prince Edward Island, growth is evidently much slower.

The distribution of growth in the growing season varies regionally, as best seen in a comparison of areas in regard to the period which produces more than half of the year's gain. In Narragansett Bay this period occurs before the middle of July (see above), at Monomoy Point it comes during the months of August and September (Belding 1931), and at Prince Edward Island it falls between mid-July and mid-September (Kerswill 1941).

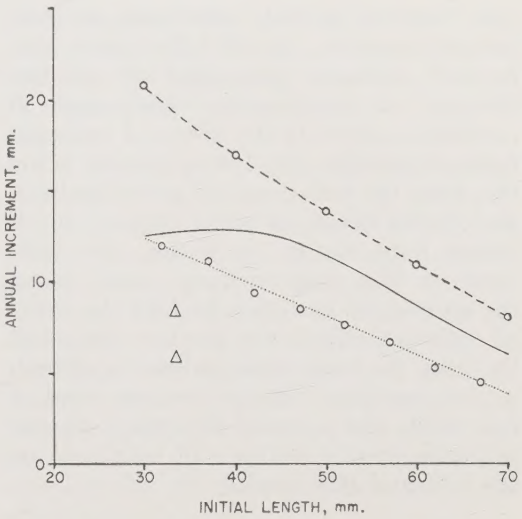

FIG. 2. Comparison of annual growth rates at four localities on the Atlantic Coast. Dashed line = Monomoy Point, Cape Cod (Belding 1931); solid line = Cape May, N. J. (Haskin 1954); dotted line = mean for Narragansett Bay; triangles = Prince Edward Island (Kerswill 1941). For explanation see text.

ENVIRONMENTAL FACTORS AFFECTING GROWTH

Volumetric growth increments are shown in Tables 4, 5, and 6, for the three years (1952–1954) in which weekly measurements of environmental conditions were made at the growth sites. The mean increments were derived by dividing the total volumetric increase by the number of animals in the population. Because previous work (Pratt 1953) had shown that the growth rate of *Venus* is influenced by the character of the sediment as well as by the properties of the water, in most cases one or more supplementary boxes containing "imported" sediments were placed at each station. For purposes of analysis the effects of water properties and of the sediment will be considered separately.

The 1952 experiments, like those of the previous years, were exploratory rather than intensive. They covered a relatively large number of localities, including an additional station not shown in Table 1, where mortality was heavy and growth negligible owing to an apparently artificial deposition of silt. (Since this was considered an unnatural condition, data from this station are omitted from the discussion.) Various "imported" sediments were used in the supplementary boxes in order to expand the range of sediments tested.

The experiments of 1953 and 1954 were designed to yield more information on the effects of specific environmental factors. Repeated measurement of the animals at intervals during the growing season greatly increased the number of possible compari-

sons between growth rates and environmental variables. In 1953 the same "imported" sediment was used at all five stations, an arrangement which made it possible to show: 1) the effects of sediment type on growth rate (water factors being the same for both boxes at each locality), and 2) the effects of water factors, which varied from station to station, the sediment in the supplementary boxes being the same at all localities. In 1954 the study of sediment effects was further intensified by using the same three sediments at each of two stations, namely a coarse sand, a fine sand, and a mud. For these reasons emphasis in this section will be placed on the 1953 and 1954 results.

Current Speed, Dissolved Oxygen Concentration, and Salinity

None of these factors appeared to be correlated with growth rates. Bottom currents were so slight that most of the readings were zero, and consequently no attempts were made to measure them after 1952. The dissolved oxygen in the bottom water averaged from 4.82 to 5.92 ml/l at the 1952 stations. Since the concentrations were apparently never critically low, this measurement also was discontinued after 1952. Average values for salinity during the three growing seasons ranged from 28.12‰ (mean for Station 2, 1953) to 31.40‰ (Station 10, 1952), and the extremes of individual readings were 21.44‰ and 31.95‰.

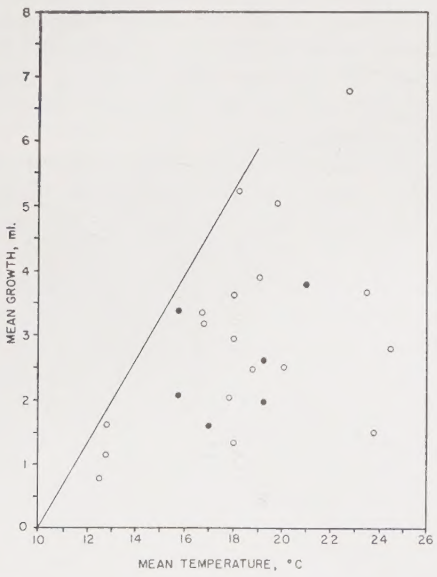

FIG. 3. Quahog growth and bottom water temperature. Open circles = mean increments (approximately 100 animals) for six-week periods in Sediment A, 1953; solid circles = mean increments reduced to six-week basis, in Sediment D, 1954. See text.

The failure to demonstrate correlations between growth and current speed, dissolved oxygen concentration or salinity, does not, of course, mean that these variables have no effect on growth. No doubt there are some environmental factors that appreciably influence growth only at values outside of the range encountered at our stations. Current speed and dissolved oxygen apparently fall in this category, the data providing insufficient range to detect the action of these factors on growth rates.

In a field study with no controls of water properties, the observed growth is the resultant of a complex of factors varying simultaneously. Under these conditions the only growth factors one can hope to detect are those so important that they influence the rate of growth in most of the environmental complexes studied. The effects of factors playing minor roles will then be obscured. Salinity is thought to have been such a minor factor in this investigation. Turner (1953a) reports that quahogs in fertilized water in tanks grew somewhat faster at salinities between 23 and 28‰ than at higher or lower concentrations, although it is not clear whether the salt content affected growth directly or by modifying the food supply. Turner's results indicate that the range of average salinities in the present study was above the optimum for growth, but evidently any differential effect of salinity in that narrow range was masked by the preponderance of other factors.

Temperature

The relation between temperature and growth rate is shown in Figure 3 in which each point represents the mean growth increment of approximately 100 animals in six weeks, plotted against the average

bottom water temperature. While the effects of temperature cannot be isolated, the action of other variables has been reduced as much as possible by plotting against the mean temperature in each growth period the average growth increments in the sediment common to all stations in 1953 (Sediment A). The 1954 data included in the figure (reduced to a six-weeks basis) are those for Sediment D, which was similar to Sediment A, especially in percentage content of the apparently important silt-clay fraction (see below). The influence of temperature is obscured by variations in other factors, with a consequent scatter of points in the graph. The figure suggests, however, that whereas growth at all temperatures may be inhibited by other variables such as food supply, the mean temperature imposes a definite upper limit to the possible rate of growth. Since other conditions were allowed to vary, this result was to be expected; a given temperature, no matter how favorable, cannot guarantee any growth at all, but on the other hand it limits the maximum possible growth rate. The line in the figure is intended to approximate this limitation. Evidently the potential growth rate increases as the mean temperature is raised from 10° to at least 23°; whether it continues to increase or falls off at higher temperatures the data are not adequate to show. A temperature most favorable for growth and a supra-optimal range could be demonstrated better in regions farther south than Narragansett Bay.

Phytoplankton

Average increments for each of the four growth periods in 1953 have been compared with the mean concentrations of phytoplankton cells found in the bottom water during the same intervals, using only the growth data from the sediment common to all stations so as to rule out the influences of bottom type on growth rate. The comparison reveals a positive correlation between quahog growth and the total phytoplankton assemblage. The relationship is such that a plot of growth rates against the logarithms of the total cell count is best described by a straight line. This means that the average growth rate increases with increasing concentrations of phytoplankton, but at a steadily diminishing rate.

To determine whether this relationship depends on the concentration of some particular fraction of the phytoplankton population, growth rates have been plotted against mean numbers of each of the four arbitrary size groups (<15, 15–37, 38–75, and >75 microns) of diatoms and of flagellates. The relationship is of approximately equal strength when growth is plotted against each of the following categories, with the indicated correlation coefficients, all of which are significant to the 1% level:

	r
Total diatoms and total flagellates	0.735
Diatoms and flagellates < 15 μ	0.750
Total diatoms	0.714
Diatoms < 15 μ	0.661

Growth rate is not significantly related to mean total flagellates, flagellates of any of the four size groups, or diatoms of 15–37, 38–75 or >75 μ. Thus the growth rate–

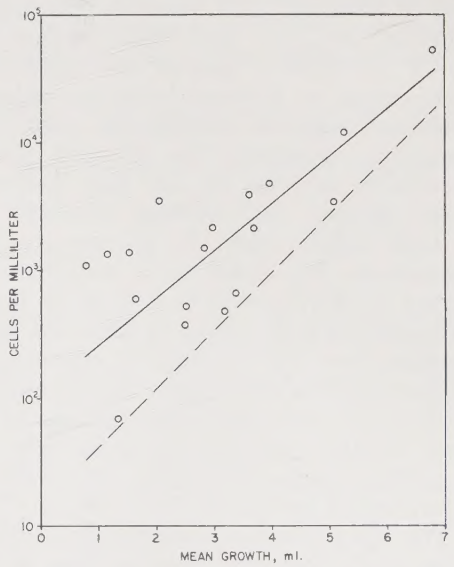

FIG. 4. Quahog growth, 1953, and the mean concentration of diatoms <15 μ in bottom water. Growth increments (average of approximately 100 animals) for six-week periods in Sediment A. Solid line is line of least squares. For explanation of dashed line see text.

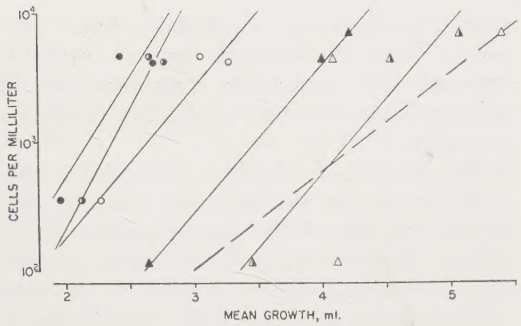

FIG. 5. Quahog growth, 1954, and the mean concentration of diatoms <15 μ in bottom water. Growth increments (average of approximately 100 animals) for eight-week periods. Circles = Station 6; triangles = Station 9; open points = Sediment C (coarse sand); half-filled points = Sediment D (fine sand); solid points = Sediment E (mud). Lines are least-squares lines. Dashed line is for open triangles.

phytoplankton correlation derives its strength from an exponential relationship between growth and the mean numbers of diatoms smaller than 15 μ (Fig. 4).

The experiments of 1954 yielded substantially the same result. Growth was again positively correlated with the mean abundance of the categories listed above, and in addition, with diatoms and flagellates of 38–75 μ, and with diatoms of 38–75 μ. Growth showed no significant relationship, or in some instances, indeed, exhibited negative correlations with the remaining categories. The strongest direct correlation appears to be that between mean growth and average numbers of diatoms smaller than 15 μ, expressed as logarithms. This relationship is shown in Figure 5, where growth in each of the three sediments at each station is indicated by a separate line. Of the negative correlations between growth and various phytoplankton groups, the most significant appears to be that relating growth to abundance of flagellates smaller than 15 μ, expressed as logarithms (Fig. 6).

The strong positive correlation between quahog growth and average numbers of the small plankton diatoms can hardly have been coincidental; a causal connection between the two variables is almost certain. The possibility of some third factor affecting the two observed variables in the same direction must not be overlooked. Concerning this possibility, all that can be said is that if such a factor exists we do not know what it is, but we do know that it is nothing that was measured. The evidence strongly suggests a direct causal connection in which the animals were deriving their nutrition largely from the small diatoms, either as living cells or as detritus after their death, and that they grew at rates approximately proportional to the concentration of this foodstuff.

If this is indeed the case, one may inquire as to what particular properties make the small diatoms important in the nutrition of the quahog. *Skeletonema costatum* was easily the predominant species involved. Of the remaining forms only *Thalassiosira nordenskioldii* and *Chaetoceros* spp. deserve mention. With such a short roster we cannot judge whether all diatoms of this size range are equally nutritious, or if at other times or places the quahog would fare as well on other species. However, since growth rates were not consistently related to other elements of the phytoplankton less than 15 μ or to diatoms greater than this size, the apparent superiority of the small diatoms as quahog food would seem to be due to both their size and their composition. Diatoms differ

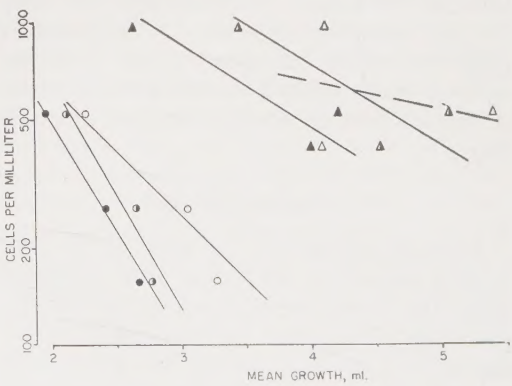

FIG. 6. Quahog growth, 1954, and the mean concentration of flagellates <15 μ in bottom water. Growth increments (average of approximately 100 animals) for eight-week periods. Circles = Station 6; triangles = Station 9; open points = Sediment C (coarse sand); half-filled points = Sediment D (fine sand); solid points = Sediment E (mud). Lines are least-squares lines. Dashed line is for open triangles.

chemically from other members of the phytoplankton in several conspicuous respects. When they are considered as a potential food (either living or as detritus), their siliceous cell walls may be a matter of indifference, whereas their high fat content (Fogg 1953) may perhaps be an enhancement. Furthermore, according to Vinogradov (1953: 154) diatoms are unique in the phytoplankton for their richness of iodine, and possibly arsenic. In this connection, the extraordinarily great concentration of iodine in *Venus* (Tressler and Wells 1924) and the high arsenic content of marine molluscs (Vinogradov 1953: 372) are suggestive.

If, then, Figure 4 illustrates the dependence of the quahog on small diatoms for its nutrition, two further points deserve brief consideration. (1) The fact that the relationship between growth and diatom abundance is exponential means that with increasing phytoplankton concentrations the animals are progressively less efficient in utilizing this foodstuff for constructive growth. The reduction in efficiency at high plankton concentrations could arise either from an inhibition of pumping or of feeding, as has been described in the oyster (summarized by Korringa 1952) or, if no such inhibition occurs in the quahog, from the animal's inability to digest all that is ingested, as in the case of copepods (Harvey, Cooper, Lebour and Russell 1935). (2) The solid line is the line of least squares and indicates average growth rates for given concentrations of diatoms when other environmental factors are allowed to vary. The dashed line is intended to approximate the maximum possible ratio of growth to the available food supply under the existing conditions, and at any given level of diatom abundance, the displacement of points to the left of this line is believed to be due to the restraint of growth by environmental influences other than the concentration of small diatoms.

The inverse relationship shown in Figure 5 suggests a possible inhibition of quahog growth by the small flagellates. Since this did not occur in 1953, the year for which more data are available, it is perhaps safer to attribute this negative correlation to other causes, such as an inverse relationship between flagellate and diatom numbers.

Sediment Type

The supplementary sediments used at two stations in 1952 and at all five stations in 1953 were, in every case, coarser than the local sediments with which they were paired. At both stations in 1952 the season's growth was considerably greater in the coarser supplementary sediment than in the local bottom material (Table 4). Table 5 reveals substantially the same result for 1953. Although in some instances growth was more rapid in the local than in the supplementary sediment for one or two growth periods, these were exceptions to the general rule. Because of the loss of some of the boxes during the fourth growth period, accumulated increments for the first three periods provide the longest series for comparison of seasonal growth in different bottom types, and on this basis growth was consistently greater in the coarser (supplementary) than in the finer (local) sediment at each locality.

In 1954 this pattern was demonstrated in a graded series of sediments, and growth rates were highest in the coarse sand, lowest

TABLE 4. *Mean growth increments (ml) for 1952*

Sediment	Station					
	2	3	6	7	9	10
Local	6.7	9.5	4.7	8.8	5.5	4.5
Supplementary	8.9	—	11.0	—	—	—

TABLE 5. *Mean growth increments (ml) for 1953, by growth period*

Station	Sediment	Growth periods*				Total periods 1, 2, 3	Total periods 1–4
		1	2	3	4		
2	2L	2.8	2.6	1.1	3.1	6.5	9.6
	A	3.4	3.7	1.5	3.6	8.6	12.2
6	6L	3.7	5.8	2.3	2.4	11.8	14.2
	A	3.2	6.8	2.8	1.3	12.8	14.1
7	7L	0.9	3.6	3.0	1.1	7.5	8.6
	A	0.8	5.2	5.1	3.0	11.1	14.1
9	9L	2.2	3.0	1.9	—	7.1	—
	A	1.1	3.9	2.5	—	7.5	—
10	10L	1.2	2.0	1.8	0.9	5.0	5.9
	A	1.6	2.0	2.5	—	6.1	—

* Growth periods (six weeks each): 1) April 27–June 7; 2 June 8–July 19; 3) July 20–August 30; 4) August 31–October 11.

TABLE 6. *Mean growth increments (ml) for 1954, by growth periods*

Station	Sediment	Growth period*			Totals
		1	2	3	
6	C	4.1	5.4	4.1	13.6
	D	3.5	5.1	4.5	13.1
	E	2.6	4.2	4.0	10.8
9	C	2.3	3.1	3.3	8.7
	D	2.1	2.7	2.8	7.6
	E	2.0	2.4	2.7	7.1

* Growth periods (eight weeks each): 1) May 24–July 18; 2) July 19–September 12; 3) September 13–November 7.

in the mud and intermediate in the fine sand (Table 6; Fig. 5).

All of these results corroborate our earlier findings (Pratt 1953), in showing a negative relationship between growth and the fineness of the sediment when fineness is expressed as percentage content of silt and clay, and also, in most cases, when other criteria of fineness are used, such as the mode of particle size distribution or the particle size corresponding to the first, second, or third quartile. Of these various measures, the one showing the most consistent relationship to growth rate is the percentage of silt and clay. The results are summarized in Figure 7, in which each line joins two points (three, for the experiments of 1954) representing growth in different sediments at the same station. In every case an increase in silt-clay content is associated with a retardation in growth, although the difference in growth rates is not proportional to the difference in silt-clay percentage.

This relationship is interpreted as meaning that the silt-clay content or some other associated characteristic of fine sediments somehow inhibits quahog growth. (The logical alternative is that some property of coarse sediments positively stimulates growth, but the nature of such a property is hard to imagine. The surface of the coarser sediments never supported a macroscopically visible growth of attached microorganisms or other organic material of potential nutritive value.) If we can assume that the silt-clay fraction or some associated factor is responsible for the slower growth in fine sediments, the problem is to determine the mechanism of the inhibition.

Observation of quahogs in aquaria showed that a distinct hole or "burrow" from the surface of the sediment to the siphon tip is by no means always maintained. Frequently the hole was partially or totally occluded with sediment, and the animal's presence could not be detected by visual examination of the sediment surface. When this is the case, any exchange of water between the animal and the watermass must be made through a layer of sediment acting as a filter. The permeability of the sediment must be an important factor whenever such filtration occurs, since if other factors remain constant, the lower the permeability of the sediment the more difficult it will be for the quahog to carry on the pumping activity essential to its respiration, excretion, and notably, nutrition. A crude but effective apparatus for measuring the relative permeabilities of sediments was therefore devised. The lower end of a six foot plastic tube two inches in diameter was loosely packed with approximately two inches of sediment held in place with a layer of No. 25 bolting silk, and the rate of flow of water under a constant head through this filter bed was determined. Permeability proved to be an inverse function of the silt-clay content (Fig. 8), with

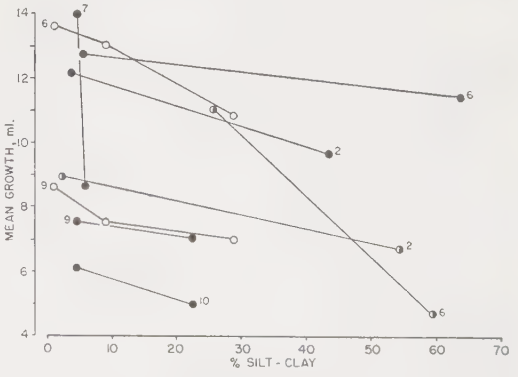

FIG. 7. Mean seasonal growth increments in pairs or series of sediments, showing the relationship between growth and the silt-clay percentage of the sediment, water properties being the same for the populations in each pair or series. Numbers refer to stations. Half-filled points = 1952; solid points = 1953 (first three growth periods); open points = 1954.

FIG. 8. Permeability and silt-clay content of sediments used in growth boxes.

a 1500-fold variation between extremes of the sediments used in the growth experiments.

It must be recalled, however, that insofar as the exchange of water between animal and watermass is concerned, sediment permeability is significant only when a well-defined burrow is not maintained. It is, therefore, interesting to note that the degree of maintenance of the burrow and the depth of burial of the animal are both related to the character of the bottom. Observations in aquaria revealed that quahogs in a mud (41.8% silt-clay) remained near the sediment surface and generally maintained an open burrow, while in coarser sediments (Sediments C, D) they were more deeply buried, and usually 40 to 90% of the animals were completely covered with sediment.

That the quahog adjusts its depth of burial to the nature of the sediment was also demonstrated by field observations. When the growth boxes were periodically raised in 1953, in the process of uncovering the animals their depths of burial in the sediment were measured. Figure 9 relates the average thickness of the sediment layer overlying the shell to the permeability of the sediment, each point representing the average depth of the 100 individuals in a box. The trend in the figure suggests a preference for an average covering of 15 or 20 mm when the permeability of the sediment will permit; in less permeable sediments, the animals are required to remain nearer the surface. When the boxes at Station 7 were raised for periodic measurement of growth, there were usually a few well-nourished starfish (*Asterias forbesi*) lying on the surface among the empty shells of several of the experimental animals recently devoured. In Figure 9 the instances in which this occurred are indicated by solid triangles. The unusual average depth of burial in these cases seems to imply that the clams were somehow apprised (tactually, or possible chemically?) of the presence of the starfish and were driven to greater depths. On one occasion the surface of the sediment in a box at Station 6 was densely overgrown with an unidentified filamentous alga. Here the average depth of burial was less than normal for that sediment (solid circle in Fig. 9), suggesting that the animals had adjusted their depth in accordance with the reduced circulation of water immediately above the bottom. The evidence therefore indicates that the potentially very great effect of sediment

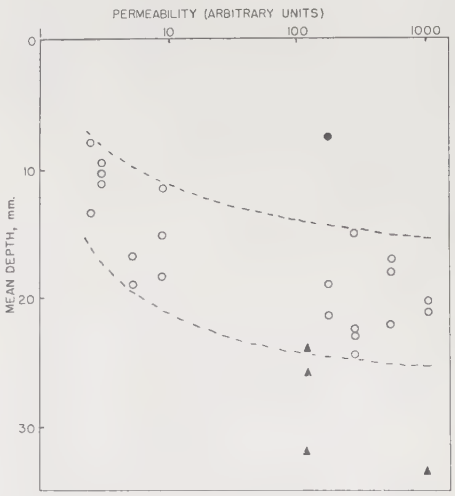

FIG. 9. Depth of burial of quahogs in sediment as related to sediment permeability. (Each point represents approximately 100 animals). Triangles denote starfish predation; solid circle, sediment surface overgrown with algae. See text.

permeability on the exchange of water between quahog and watermass is perhaps largely offset by the animals' shallower burial and better maintenance of burrows in the finer sediments.

An alternative hypothesis to explain the slower growth in fine sediments assumes a direct effect of the sediment on the quahog's tissues. Since the shell valves must be parted when the siphon is protruded, the animal cannot pump water without exposing at least the edges of the mantle to the surrounding medium. The decomposition of organic matter in fine sediments may result in the accumulation of substances directly deleterious to the soft parts of the animal in contact with the sediment. The relative impermeability of the finer sediments would intensify this effect by reducing the rate of exchange of the interstitial water in the sediment with the water above.

A thorough evaluation of this theory would require quantitative analyses for an unknown number of hypothetical substances. Rather than attempting such a task, measurements were made of one factor only, the sediment pH, since it seemed quite possible that the inhibition of growth in fine sediments might be mediated by an accumulation of hydrogen ion itself or of other substances associated with acid conditions. Attempts to measure pH in the field were not satisfactory. As soon as the boxes were raised and brought aboard, small samples of the sediment were removed and the pH immediately determined with a Beckman pH meter, but the change in water content (a function of permeability) varied so much from sediment to sediment that no reliance could be placed in the results.

In 1954 a sea water aquarium system was assembled in a shanty at the end of the Laboratory dock, to supplement the field studies and to make possible additional observation on the behavior and growth of quahogs in different sediments. Unfiltered water was pumped continuously into aquaria containing substantially the same three sediments as used in the experimental boxes for that year. (The "coarse sand" and "fine sand" were identical with Sediments C and D, respectively, of the boxes; the "mud" had a higher silt-clay content, as shown in Table 2.) The water, which was about seven inches deep in the aquaria, flowed at a slow and constant rate without disturbing the sediments. Twenty quahogs were placed in each aquarium. They buried themselves within a few hours and behaved apparently quite normally. Aquarium water temperature was continuously recorded with a Bristol recording thermograph and various observations were made over a period of two months during which the animals were not disturbed. The aquarium studies were cut short by the loss of the sea water system and experimental animals in the August 31 hurricane. This precluded certain observations (such as dissolved oxygen measurements at the sediment—water interface), and unfortunately there is no record of growth as the animals had not been remeasured. The studies that were completed are summarized below.

The pH of the aquarium sediments was determined *in situ*, using the Beckman meter with a glass electrode inserted di-

TABLE 7. *pH values in aquarium sediments*

Depth in sediment	Coarse sand*				Fine sand†				Mud*			
	Min.	Max.	Range	Mean	Min.	Max.	Range	Mean	Min.	Max.	Range	Mean
mm												
15	6.60	7.39	0.79	7.09	6.73	7.32	0.59	6.91	6.55	7.34	0.79	7.08
25	6.45	7.35	0.90	7.03	6.55	7.27	0.72	6.76	6.55	7.40	0.85	7.05
40	6.51	7.35	0.84	6.97	6.35	7.25	0.90	6.65	6.81	7.41	0.60	7.12
75	6.50	7.05	0.55	6.68	6.15	6.85	0.70	6.53	6.90	7.43	0.53	7.14
Grand averages				6.94				6.71				7.10

* Ten series of determinations.
† Twelve series of determinations.

rectly into the sediment to various depths and a calomel reference electrode in the water above. Measurements were made at evenly scattered points in the aquaria over a period of several days at water temperatures of 20.0–22.0°C, the pH of the water ranging between 7.60 and 7.88. Average pH values for the three sediments did not prove to be substantially different (Table 7); in all but one series of determinations at a particular depth, the range of pH values in each aquarium was greater than the difference between the mean values for that depth in any pair of aquaria. Furthermore, the expectation that the mud, which was black with organic matter, would prove more acid than the clean sands was not realized: indeed it was slightly more alkaline. Insofar as conditions in the aquaria simulated the natural environment, it can be stated that the inferior growth in fine sediments is not due to an accumulation of acids. That some other growth inhibitory substances may occur in fine sediments remains a possibility as yet untested.

In addition to differences in sediment permeability and the possible accumulation of injurious chemical agents in mud, a third factor that may at least in part account for the inferior growth in fine sediments involves the quahog's behavior. Loosanoff and Tommers (1948) have shown that suspended silt has a marked effect on the pumping rate and hence on the feeding of oysters; as little as 0.1 g of silt per liter of water reduced the average pumping rate 57 %, and the oysters expelled large amounts of silt as pseudo-feces. Quahogs probably react in a similar manner. Individuals living in mud must inadvertently take in considerable amounts of silt and clay, which can be presumed to be in suspension immediately above the bottom wherever currents roil the surface of the sediment. Perhaps most of the fine sediments taken in are particles dislodged by the powerful inhalant stream as the water is drawn down through the mud into the siphon. The intricate mechanism by which such sediment particles are separated from the animal's food and expelled as pseudo-feces, an indispensable adaptation to a filter-

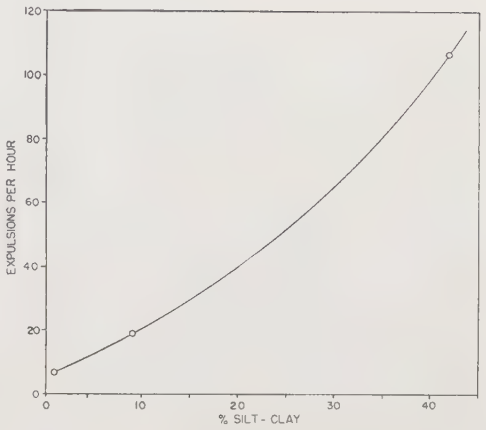

FIG. 10. Average rate of expulsion of pseudo-feces by quahogs as a function of the silt-clay content of the sediment.

feeder immersed in shifting sediments, has been described in detail by Kellogg (1915). This process must result in an additional expenditure of energy, a reduction in actual feeding time, and probably the loss of some nutritive particles incompletely separated from the indigestible matter expelled. No feasible method for fully testing this theory presented itself. However, since the discharge of pseudo-feces proved to be readily detectable as a visible stream or cloud, the critical question, whether or not quahogs in mud do in fact expel pseudo-feces much more often than do those in sand, could be answered by direct observation. The three aquaria were watched simultaneously for 30-minute periods, and the number of expulsions noted. Eleven such periods of observation, in all phases of the tidal cycle and with the temperature varying only between 18.5 and 20.6°C, produced the following average numbers of expulsions per 30-minutes: coarse sand, 3.4; find sand, 9.5; and mud, 53.4 (Fig. 10). This strongly suggests that one reason (possibly the principal reason) for the inferior growth of *Venus* in the finer sediments is the necessity of frequent clearing of the animal's filtering apparatus, with a consequent expenditure of energy and interference with the feeding process.

The retarding of growth in fine sediments is probably the combined expression of several factors. That the effect is more con-

sistently related to the silt-clay content than to any other sediment parameter measured implies at least an indirect causal connection between growth and this or some closely allied property of the sediment.

Of the various possible mechanisms discussed, (1) the great reduction in permeability associated with high silt-clay percentages in theory could minimize the exchange of water between quahog and watermass although in practice the animals' shallower burial and clearer definition of burrows evidently compensates in large measure for this direct effect of sediment impermeability; (2) the production in mud of harmful substances other than acids remains a possibility, and such an effect would be augmented by the reduced rate of flushing in fine sediments; and (3) the high rate of expulsion of pseudo-feces required of animals embedded in fine sediments presumably interrupts their feeding, consumes energy that might otherwise be used in constructive growth, and hence retards the growth rate.

SUMMARY

Quahog growth rates in Narragansett Bay have been observed over a five-year period, by use of retrievable boxes placed on the bottom, containing natural sediments and individually identifiable animals. Data from 10 localities have produced the following facts relative to variations in growth rate:

1. If growth is expressed in terms of shell length, average growth increments are inversely related to initial length, animals of initial length 35 mm growing approximately three times as fast as animals of 70 mm; however, the average volumetric increase is approximately constant over this size range.
2. Average growth rates in different parts of Narragansett Bay show variations up to nearly threefold in any given year.
3. Over a four-year period growth rates at the individual stations generally varied but little from year to year.
4. In most cases more than half of the year's growth occurs before mid-July.
5. Annual growth rates in Narragansett Bay are considerably higher than at Prince Edward Island and appear to fall in the same general range as those reported for New Jersey and the south side of Cape Cod.

During three years and in diverse environments growth rates in the field have been compared with prevailing physical, chemical, and biological conditions in the hope of identifying the principal environmental factors controlling growth. The results are summarized as follows:

6. Growth was not appreciably influenced by existing differences in the current speed, dissolved oxygen content, or the salinity of the bottom water.
7. Growth is negligible below 10°C and increased with rising mean temperatures at least to 23°C. Temperature appears to impose an upper limit to the potential rate of growth.
8. Growth rates proved to be a function of the abundance of small plankton diatoms, a correlation which is interpreted to mean that this constituent of the phytoplankton, either living or as detritus, is an important source of quahog nutrition in our waters.
9. When different sediments were used in pairs (seven experiments) or in gradients of three sediment types (two experiments), water properties being the same for each combination of sediments, growth was consistently slower in the sediments with the higher silt-clay content, although growth rates were not strictly proportional to this or any other observed property of the sediment. The relation between growth rate and silt-clay content of sediment is discussed with reference to sediment permeability and the possible accumulation of growth inhibitory substances in muds. Aquarium observations have shown a direct correlation between the silt-clay content of the sediment and the rate of expulsion of pseudo-feces, and it is argued that the

inhibition of growth in fine sediments may result in part from the interruption of feeding and the additional expenditure of energy occasioned by the necessity for frequent clearing of the animals' filtering apparatus.

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Algal Indicators of Trophic Lake Types

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ABSTRACT

The dominant species of algae in the Great Lakes and in the large oligotrophic lakes of western Canada are not those commonly quoted as oligotrophic indicators. It is suggested that this apparent discrepancy may be due to the lack of sufficiently detailed taxonomic information, to the non-existence of oligotrophic indicators, or to the fact that oligotrophy of these lakes is essentially morphometric rather than edaphic. The utility of phytoplankton quotients and the problem of numbers of species versus dominant species are discussed.

INTRODUCTION

Early recognition of differences in the quantity and quality of plankton in lakes contributed to the origin of the trophic system of lake classification. The trophic system has continued to evolve and at the same time, there have been developments in the recognition of plankton types. These have been mainly concerned with the phytoplankton and include the use of a variety of indices and quotients. This field has been developed mainly by European workers with, as yet, little application to the waters of North America.

Phytoplankton studies in the Great Lakes and in the large oligotrophic lakes of Western Canada have revealed a species composition which disagrees in many respects with that commonly quoted as typically oligotrophic. A recent study of the plankton of Great Slave Lake (Rawson 1956) has brought this apparent anomaly to our attention. Thus it has seemed desirable to consider present knowledge and theories concerning phytoplankton indicators and especially their application to the oligotrophic lake type.

EUTROPHIC VS. OLIGOTROPHIC PLANKTON

The usual scheme for distinguishing oligotrophic from eutrophic plankton is indicated in Table 1. First we should remind ourselves that these types are not mutually exclusive. We may prefer either to think that in the wide sense they overlap considerably, or, that between the two types in their narrower sense, lies a third or mesotrophic type.

Looking at the characteristics in Table 1, we have first the quantity. It is relatively easy to demonstrate the heavy plankton of eutrophic as contrasted to the thin or poor plankton of oligotrophic lakes. An illustration of this is provided in a recent account (Rawson 1953) of the standing crop of net plankton in lakes of Western Canada. In this paper a graph shows the average standing crop of net plankton in twenty lakes plotted against mean depth. In the typical eutrophic lakes, with mean depths of less than 20 metres, the dry weight of plankton is from 50 to 200 kg/ha while in the deeper, oligotrophic lakes the average is usually between 10 and 30 kg/ha. There are of course numerous intergrades (mesotrophic?) but the typical eutrophic lakes of this group have at least 5 times as much plankton as the typical oligotrophic lakes.

Returning to Table 1, we have the second feature, variety of species. The differentiation here is not so clear as in the quantity of plankton. The implication is that many species but small numbers occur in oligotrophy and few species but great numbers in eutrophy. In practice eutrophic lakes also seem to have many species and it is difficult to distinguish sharply between the fewer limnetic species and the richer variety of the inshore areas. The greater depth distribution of the plankton in oligotrophic and the more concentrated and restricted trophogenic layer in eutrophic lakes is a real difference but not one that is easily measured. Likewise the extent of diurnal vertical migrations is not readily determined nor particularly

TABLE 1. *Plankton of oligotrophic and eutrophic lakes*

	Oligotrophic	Eutrophic
Quantity	Poor	Rich
Variety	Many species	Few species
Distribution	To great depths	Trophogenic layer thin
Diurnal migration	Extensive	Limited
Water-blooms	Very rare	Frequent
Characteristic algal groups and genera	Chlorophyceae (Desmids if Ca-) *Staurastrum* or Diatomaceae *Tabellaria* *Cyclotella* Chrysophyceae *Dinobryon*	Cyanophyceae *Anabaena* *Aphanizomenon* *Microcystis* and Diatomaceae *Melosira* *Fragilaria* *Stephanodiscus* *Asterionella*

useful as an index. The frequent occurrence of water blooms in eutrophic and their absence from typical oligotrophic lakes is not questioned. Of course the intensity of blooming in a particular lake may vary from year to year, and a strongly eutrophic lake may not have a convenient bloom at the time of investigation.

It is with the last group of characters that we are chiefly concerned, i.e. those larger groups, genera and species of algae that may be helpful as indicators of the trophic character of lakes. It is here that we have found numerous difficulties, especially with the phytoplankton of those very large oligotrophic lakes which we have been investigating (e.g. Great Slave Lake, Rawson 1956). In these lakes the blue-green algae are scarce and water blooms absent, but the remaining features do not fit the conventional scheme. Desmids, considered as characteristic of oligotrophy, are not abundant, perhaps because the waters are not particularly low in calcium. The diatoms are distinctly dominant, but in many lakes and especially in Great Slave Lake, the dominant genera of diatoms are those usually associated with eutrophic conditions. *Dinobryon*, considered by some authors as an oligotrophic indicator, is common but not constant and rarely dominant. It was these discrepancies which led us to look more closely into the question of algal indicators of trophic condition.

VARIETY VS. DOMINANCE

Before beginning a discussion of plankton indicators it may be desirable to point out that some confusion has resulted from two very different approaches. On the one hand attempts have been made to characterize plankton by the *number of species present*, regardless of whether these species are represented by few or many individuals. In contrast to this, we have the search for *ecological dominants* and concurrent attempts to classify and name communities or associations by their dominant species. Thus, for instance, the plankton of an oligotrophic lake is said to be characterized by desmids, meaning that it contains many *species* of desmids but the plankton sample may be dominated by diatoms. This is a very common situation in our oligotrophic lakes. The variety of desmid species may well be present but one has to search for them, while a few species of diatoms commonly make up 80 or 90 per cent of the cells present. As a second example, we say that eutrophic plankton is characterized by blue-green algae. Here we are probably thinking not of numbers of species, but of the tremendous numbers of individuals of a few species as in a water bloom. Nevertheless, as suggested above, it may not be safe to assume that eutrophic plankton is poor in species. It may only seem so because the rarely occurring species are very difficult to find among the few abundant forms.

The concept of species richness has been used extensively in describing plankton communities. Moreover the relative numbers of species representing different taxonomic groups in a plankton sample has been found significant of ecological conditions. Thus, in eutrophic lakes the number of species of Chlorococcales is likely to exceed the number of species of Desmidiaceae, while in oligotrophic lakes the reverse condition is found. This leads to the calculation of quotients which will be considered later. It should be pointed out that any approach involving the determination of the number of species present is subject to certain practical dif-

ficulties. It is generally agreed that, in describing lake plankton, one should count only euplankters, i.e. those described as pelagic or limnetic. In practice it is often very difficult to segregate these from the inshore or even attached forms which have been carried into the open water. Also, when "rare" species are included, the number of species recorded will vary greatly depending on the intensity of the search and the season at which the sample is collected.

Emphasis on the ecological dominants in the plankton community leads to an entirely different procedure. Rare species tend to be ignored, and, when counting to determine the composition of the plankton, it is sometimes not feasible to separate species which resemble each other closely. The ecologist is likely to be more interested in the percentage composition of the plankton population than in the number of species present. He may attempt to name or describe the community by reference to the most abundant and constant species, e.g. Thunmark's (1945) reference to the *Microcystis aeruginosa – Daphnia cucullata* community. However, with respect to trophic classification, it appears that the dominant species are often those with rather wide tolerance (eurybionts) and thus they may be even less significant of trophic condition than the less frequent species. It may be added that counts which show the numerical percentage of different species in terms of total cells, may also be somewhat misleading since the cell size of different algae varies greatly. Thus calculation of unit and percentage volumes may provide a different picture of "dominance". This may be illustrated by a brief reference to Table 2 which summarizes a large number of plankton counts from Great Slave Lake (Rawson 1956). In general, the discrepancy between numerical and volumetrical percentages is even greater among the zooplankters than in the algae. In the main lake *Melosira* contributes 74 per cent numerically and 83 per cent by volume, *Asterionella* 16 per cent numerically and 4 per cent by volume. However in the east arm *Asterionella* is numerically dominant with 60 per cent, but *Tabellaria* might also be considered dominant since it contributes 49 per cent of the volume.

TABLE 2. *Composition of net plankton, Great Slave Lake*

	67 hauls, Main Lake 1946–1954			12 hauls, East Arm 1946–1947		
	Average numbers	% numbers	% volume	Average numbers	% numbers	% volume
Entomostraca						
Nauplii	3,219	47	1	1,733	70	2
Diaptomus	2,403	35	38	367	15	20
Cyclops	742	11	11	197	8	9
Limnocalanus	374	6	49	129	5	55
Senecella	+	+	+	11	+	10
Daphnia	34	1	1	25	1	4
Total	6,772			2,465		
Rotifera						
Keratella	1,250	38	1	15	12	1
Kellicottia	871	26	1	42	34	3
Synchaeta	513	16	1	7	6	1
Asplanchna	473	14	96	7	6	92
Polyarthra	198	6	+	1	1	+
Conochilus	+	+	+	50	41	3
Total	3,305			122		
Phytoplankters (Cells)						
Melosira	7,619,000	74	83	1,370	3	4
Asterionella	1,597,000	16	4	27,267	60	18
Dinobryon	486,000	5	3	10,576	23	17
Fragilaria	351,000	3	+	514	1	+
Tabellaria	165,000	2	8	3,791	8	49
Eunotia	+	+	+	1,471	3	+
Total	10,218,000			44,989		
Phyto-: zooplankton vol.	1:19			1:445		

It is hardly necessary to suggest that reliable observations of species numbers or individual numbers should be based on collections extending through a considerable portion of the season. However, an examination of the literature reveals many instances of classification of plankton and calculation of quotients based on single collections. The extent of seasonal changes in the dominance of phytoplankters may be illustrated from Hutchinson's (1944) account of the phytoplankton of Linsley Pond. In 1937 a spring maximum of the diatom *Synedra* was

From the foregoing comments it would seem that both approaches, i.e. species numbers and numbers of individuals, have certain advantages and limitations. Thus minute data as to the species and varieties present and detailed analysis of the percentage composition of the population are both desirable.

TABLE 3. *Phytoplankton quotients*

Simple quotient—

$$\frac{\text{Number of species of Chlorococcales}}{\text{Desmidiaceae}} = \begin{matrix}\text{if } <1, \text{ oligotrophy} \\ \text{if } >1, \text{ eutrophy}\end{matrix}$$

Compound index, Nygaard (1949)

$$\frac{\text{Myxophyceae} + \text{Chlorococcales} + \text{Centrales} + \text{Engleniaceae}}{\text{Desmidiaceae}} =$$

if <1, oligotrophy
if 1 – 2.5, mesotrophy or slight eutrophy
if >2.5 true eutrophy

Diatom quotient, Nygaard et al.

$$\frac{\text{Centrales}}{\text{Pennales}} = \begin{matrix}\text{if 0 to 0.2 oligotrophy} \\ \text{if 0.2 to 3.0 eutrophy}\end{matrix}$$

followed by a sudden increase in *Dinobryon* and later by *Fragilaria* and the blue-greens *Anabaena* and *Oscillatoria*. A single analysis of the plankton on June 1, the time of the *Dinobryon* maximum, would have given an impression of the trophic nature of the lake very different from that obtained on August 17, at the time of the *Anabaena* maximum. In this connection it should be noted that Nygaard (1949) suggests that the use of chlorophycean and compound quotients (see Table 3) be confined to the months of June to August, whereas the diatom quotient may be applied at any season.

ARE THERE INDICATORS OF OLIGOTROPHY?

A considerable number of algal species appear to be limited to eutrophic waters but very few can be named as oligotrophic indicators. Järnefelt (1952) in a very thorough study of more than 300 lakes in Finland, lists some 30 species of plankters found only in eutrophic lakes but only 6 which were limited to oligotrophic waters. Several possible explanations might be offered for this apparent scarcity of oligotrophic forms.

A first possibility is that true oligotrophic indicators do not exist. It seems reasonable that the so-called eutrophic forms should thrive in water rich in nutrients and disappear when the available nutrients fall below a minimum requirement. It may be less easy to conceive of species which thrive in low concentrations of nutrients but are unable to tolerate slightly higher amounts. There are, of course, species which are cold stenothermal, but low temperatures, although they often accompany nutrient deficiency, are not necessarily indicative of oligotrophy. It may be that most of the species in oligotrophic plankton are not distinctive of that condition but simply the residue of widely tolerant forms which thrive also under meso- or even in eutrophic conditions. However, a few species are believed to prefer lower concentrations of nutrients. Rodhe (1948) concluded both from field observations and laboratory experiments that *Dinobryon divergens* and *Uroglena americana* prefer low concentrations and are inhibited by rather small additions of phosphates.

It is possible also that algae limited to oligotrophic waters exist and that we have difficulty in recognizing them. It seems reasonable that from widespread species there might develop two or more varieties (ecotypes?) adapted to special conditions. A well known example of this is Ruttner's (1939) discovery of two varieties of *Asterionella formosa*, one *A. f. hypolimnetica* found in cold water, 5–8°C, and the other *A. f. epilimnetica* tolerating temperatures of 7–14°C. These varieties were distinguishable only by careful measurement and their cell lengths overlap. Perhaps in some cases physiological races have developed which show little or no morphological differentiation. A related and serious problem for the limnologist is the frequency with which expert algologists disagree as to the trophic preference of algal species.

A third problem concerns the distinction between fundamental edaphic oligotrophy and so-called secondary or morphometric oligotrophy. It seems probable that our very large, deep lakes of North America are oligotrophic mainly because of their morphometric factors (Rawson 1955). In some of them climatic and edaphic situations augment the degree of oligotrophy. Perhaps certain phytoplankters respond to shortage of nutrients and thus indicate the edaphic situation. Great depths and low temperatures could result mainly in reducing the number of plankters rather than elimination

of species. If this is so perhaps we should not be surprised to find Great Slave Lake plankton dominated by a *Melosira* which is certainly not regarded as an oligotrophic indicator. It could be that in the main part of Great Slave Lake, the favourable edaphic effect of a tremendous contribution of nutrients by the Slave River moderates to a considerable degree the oligotrophy that would have resulted from great depths and low temperatures. Reference will be made below to the dominance of *Asterionella* in the east arm, which is not affected by the inflow of the Slave River and has thus a much lower mineral content.

ARE PHYTOPLANKTON QUOTIENTS USEFUL?

The relative numbers of species of Chlorococcales and Desmidiaceae present in particular lakes have been used to recognize trophic types. In practice the number of species of Chlorococcales is divided by the number of desmids and the quotient, if less than one, is said to indicate oligotrophy or if greater than one, eutrophy (Table 3). The problem of satisfactory determination of the number of species present has been referred to above but, aside from this limitation, the quotient does provide a means of expressing the degree of species dominance of desmids in oligotrophic and of Chlorococcales in eutrophic lakes.

In the net plankton of Great Slave Lake we found 18 Chlorococcales species and 26 desmids, a quotient of 0.7 which would suggest oligotrophy, a condition which certainly exists in this lake. However, many of the species listed were found in the shallow, inshore areas and none of them occurred in sufficient numbers for effective counting in determining the total phytoplankter cells. It may be possible to differentiate between "characteristic" and "dominant" species but it seems rather odd to determine the trophic situation from desmids and Chlorococcales when the diatoms are making up 95 per cent of the phytoplankter cells (Table 2 above).

Quotients have been used extensively by Scandinavian workers and especially by the Danish investigator Nygaard. In 1949 he proposed the compound index, determined by dividing the total number of species of Myxophyceae, Chlorococcales, Centrales and Eugleniaceae by the number of species of Desmidiaceae. Nygaard felt that this provided a better indicator of the trophic type than the simple quotient. Applying it to the net plankton of Great Slave Lake we have $\frac{16 + 18 + 9 + 0}{26} = 1.65$ which according to Table 3 indicates mesotrophy. However, if only those species collected in the open water are considered we have $27 \div 5 = 5.4$, which would be regarded as distinctly eutrophic, but other data for Great Slave Lake show it to be distinctly oligotrophic.

A third quotient, for diatoms, is derived from the number of species of Centrales over that of the Pennales. In Great Slave Lake this again would suggest a eutrophic condition.

In these last two quotients abundance of Centrales is considered as evidence of eutrophy. However, we should note that Foged (1954) working on lakes in central Denmark, found evidence that among the Centrales, *Cyclotella* points toward oligotrophy, *Melosira* indicates eutrophy, and *Stephanodiscus* more pronounced eutrophication.

It is noteworthy that Järnefelt (1952) does not find quotients reliable in his intensive studies of Finnish lakes. Also Nygaard (1955) after a careful test of his own compound index, using photosynthetic activity as an indicator for trophic type, found that the index gave good agreement at the extremes of the trophic range but was erratic in the middle. If quotients are reliable only at the extremes of the trophic scale it would seem that they can be of limited use since in such cases the differentiation is usually obvious without making any calculation. However, Nygaard is continuing his investigations and hopes to improve the use of his index. Brook (1955) has also found it useful in a study of some Scottish waters. It is possible that the quotients give more reliable results when applied to lakes of a somewhat restricted geographical region rather than to a group of large and wide-spread lakes such as those

discussed below. Much more investigation will be needed before a fair evaluation of the quotient hypothesis can be made.

ZOOPLANKTER INDICATORS

If it is found that certain species of algae can be used as indicators of trophic condition it would seem reasonable that some zooplankters could also serve this purpose. American limnologists seem to have given little attention to this question but the European literature contains numerous interesting references. Järnefelt (1952) lists a few species of Cladocera and a number of rotifers as confined to eutrophic lakes in Finland. *Bosmina longirostris* was found only in eutrophic and *B. obtusirostris* only in oligotrophic lakes. Certain species of the rotifer genera *Polyarthra*, *Keratella* and *Trichocerca* seemed to show distinct trophic preference. In Sweden, Thunmark (1945) cited *Daphnia cucullata* as strongly eutrophic, *Diaptomus gracilis* and *Bosmina longispina* as oligotrophic.

In Great Slave Lake the oligotrophic species *Bosmina obtusirostris* is common, but so also are two rotifers *Keratella quadrata* and *Asplanchna priodonta* which are considered to show eutrophic affinities in European waters.

Some of the zooplankters which might be considered characteristic of our oligotrophic lakes are probably confined to these lakes for reasons other than low nutrient concentrations. Thus cold stenothermal copepods such as *Limnocalanus macrurus* and *Senecella calanoides* are limited to oligotrophic lakes, but their distribution may be the result of glacial history rather than trophic preference.

DOMINANT PHYTOPLANKTERS IN LAKES OF WESTERN CANADA

It was stated above that the writer's interest in the problem of phytoplankton indicators was stimulated by his attempts to interpret findings on Great Slave Lake. This led to a review of observations made over a period of years on lakes of Western Canada. Considering the dominant species rather than the number of species present, it has been possible to prepare a list in which these dominants are placed in approximate sequence from oligotrophic to eutrophic occurrence. It should be made clear that by dominance we mean contributing a high percentage of the phytoplankter count over much of the summer season. The result is presented in Table 4. This is a tentative list, and no great certainty is implied as to the position of any species. However, it is based on observations of many lakes and over a 25-year period. With further revision and verification it may acquire some degree of utility.

TABLE 4. *Approximate trophic distribution of dominant limnetic algae in lakes of Western Canada*

Oligotrophic	Asterionella formosa
	Melosira islandica
	Tabellaria fenestrata
	Tabellaria flocculosa
	Dinobryon divergens
	Fragilaria capucina
	Stephanodiscus niagarae
	Staurastrum spp.
	Melosira granulata
Mesotrophic	Fragilaria crotonensis
	Ceratium hirundinella
	Pediastrum boryanum
	Pediastrum duplex
	Coelosphaerium naegelianum
	Anabaena spp.
	Aphanizomenon flos-aquae
	Microcystis aeruginosa
Eutrophic	Microcystis flos-aquae

Asterionella formosa is placed at the oligotrophic end of the scale. Diatoms are consistently dominant in the phytoplankton of the many oligotrophic lakes examined by the writer in Western Canada. These are almost always of three genera, *Asterionella*, *Melosira* and *Tabellaria*. Note that *Cyclotella*, often found in highly oligotrophic lakes in Europe, is not dominant or even common in this group. Of these three, *Asterionella formosa* is found regularly in the most oligotrophic lakes such as Reindeer and Athabaska in northern Saskatchewan, Great Bear in the Northwest Territories, Maligne and Pyramid in Jasper National Park, and Waterton Lake in southwestern Alberta. It should be noted that all of these lakes are very low in minerals, ranging from 60 to 104 ppm. Olive (1955) has also found *Asterionella* dominant in the very high

altitude lakes of Colorado. Perhaps the most convincing evidence for considering *Asterionella* as more oligotrophic than *Melosira* comes from Great Slave Lake (Rawson 1956) and Lac la Ronge, Saskatchewan. Both of these lakes are oligotrophic but each has at its east end a large bay which is much deeper, colder and lower in nutrient minerals. In both of these lakes, and through several summers, *Melosira* continued as the dominant phytoplankter but *Asterionella* has been dominant in the more oligotrophic associated bays. It is obvious that the variety or varieties of *Asterionella formosa* occurring in these lakes should be determined.

The *Melosira* of Great Slave Lake is *M. islandica*, and Ahlstrom (1936) found that this species was dominant also in Lake Michigan. Most, but not all, algologists seem to agree that *M. islandica* is less eutrophic than the more common *M. granulata*. Hustedt (1942) indicates that *M. islandica* var. *helvetica* is found in oligotrophic lakes of alpine and northern regions. Since *M. granulata*, a widely recognized eutrophic indicator, seems out of place in very large oligotrophic lakes such as Michigan, Superior and Nipigon, one is led to speculate that in at least some of these cases the species collected was actually *M. islandica*.

The two species of *Tabellaria*, *fenestrata* and *flocculosa*, are found in most of our oligotrophic lakes and are dominant in a few alpine lakes in the Rocky Mountain region of Alberta. Teiling (1955) regards *T. flocculosa* as the more oligotrophic of the two species, but in our lakes neither seemed consistently more oligotrophic in its distribution than the other. *Fragilaria capucina* however was definitely more oligotrophic than *F. crotonensis*, which is regarded as mesotrophic or even eutrophic. This was clear in Great Slave Lake where *F. capucina* is the common and widespread species, while *F. crotonensis* was abundant only in restricted inshore areas, usually warmer and with more nutrients than the open lake.

Stephanodiscus niagarae is numerous and widespread in our lakes but only occasionally a temporary dominant. It is found both in oligotrophic and eutrophic lakes and thus comes in the mesotrophic range of our list.

It is not necessary to review in detail the evidence which lead to assembling the remainder of the list. The three blue-green genera seem to lie quite definitely at the eutrophic extreme, and, unlike the three diatoms at the other end of the scale, no special significance is attached to their order of listing. Perhaps more detailed work on our eutrophic lakes would suggest some sequence here.

CONCLUSION

The usual criteria for distinguishing oligotrophic and eutrophic plankton have been examined and the utility of certain indices questioned.

It is suggested that the numbers of species of certain groups present in a plankton sample would seem to have less ecological significance than the numbers of individuals of the dominant species.

The question has been raised as to whether the scarcity of reliable oligotrophic indicators among the algae may be because (a) such indicators do not exist, (b) we are failing to recognize them taxonomically, or (c) the so-called oligotrophic indicators respond chiefly to edaphic influences and thus may not appear in lakes whose oligotrophy is mainly of morphometric or climatic origin.

The opinion is expressed that phytoplankton quotients are at present of rather limited use to the limnologist.

An attempt has been made to arrange the dominant phytoplankters of lakes in western Canada in order of their occurrence from oligotrophy to eutrophy. The list is tentative but may be capable of revision into a useful guide. Intensive taxonomic studies and especially varietal determinations of the characteristic species are greatly needed. The writer would be pleased to make extensive collections available to interested algologists.

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Population Dynamics of the Marine Clam, *Mya arenaria*[1]

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ABSTRACT

From present spawning and survival data, it is calculated that stable local populations of *Mya* require an average annual production, per spawning pair, of 40 spat which both survive and remain in the spawning area. The sizes of larva populations which survive and remain in the area under various flushing rates and mortalities are calculated. From this and the 40 spat/pair/year level the suitability of estuaries or embayments as sites for *Mya* cultivation may be judged when local flushing rates and mortality coefficients are known. A formula for estimating the harvestable fraction of the existing population under local flushing rate and mortality conditions has been derived. The method, combined with the local oceanography, adequately explains the anomalous history of *Mya* production in the harbor of Barnstable, Massachusetts.

INTRODUCTION

The soft-shelled or "steamer" clam, *Mya arenaria*, formerly a wildlife resource of great value, has been reduced by overexploitation to such an extent that a high degree of management practice must be developed and put into effect if this food delicacy is not to disappear from the market. A few empirical management practices are employed but underlying fundamental studies, to serve as their guides, are lacking.

Certain principles for determination of environmental suitability and size of the harvestable fraction of the population evolved in this study appear to be applicable not only to *Mya* but, with modification, also to other species both marine and freshwater.

In the waters of Massachusetts *Mya* larvae spend about a fortnight in a weakly-swimming pelagic larval stage prior to settling to the bottom as spat and assuming their burrowing mode of life. During their swimming stage they are at the mercy of the currents and are subject to enormous mortality from a variety of causes, including predation. *Mya* is primarily an inhabitant of estuaries and tidal embayments where its larva populations are reduced by being flushed out to sea by the tides, in addition to the mortality from all causes which would occur regardless of tidal action.

This study is concerned with the reductions in numbers of larvae that result from the combined effects of flushing-out and mortality. From consideration of these matters come indications of some of the criteria by which we may judge the suitability of estuaries or embayments as localities for *Mya* cultivation. A formula for the size of the harvestable fraction of existing populations is derived. The considerations are finally applied to an embayment whose *Mya*-producing history is known. In conjunction with knowledge of the local oceanography, they appear to explain this history adequately.

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GENERAL CONSIDERATIONS

Mya Biology

Adults of *Mya* are not hermaphroditic; male and female individuals are separate. Spawning is presumed to occur in massive

[1] Contribution No. 766 from the Woods Hole Oceanographic Institution.

bursts probably involving all the adults of an area. For the purposes of this paper the annual spawning is considered to be complete in the one major burst per year. Belding (1930) calculated that a single female *Mya* produces three million eggs per year. Since the author knows of no evidence of abnormal sex ratios in this species, it is assumed that spawning involves equal numbers of males and females, and further, the mass spawning is presumed to result in fertilization of all the eggs. A single spawning pair is considered to produce three million larvae per annual spawning.

The studies of H. J. Turner (personal communication) indicate that only about 1% of the spat which settle to the bottom at the end of the 14-day swimming stage will survive to become sexually mature. If two second-generation adults (to replace the original parent pair) are to result from this 1% survival, 200 spat must settle.

Observations by the author indicate that five years is a conservative estimate of the period of sexual maturity in *Mya*. In a stable population each pair of parent *Mya* must, during its period of sexual maturity, replace itself with a second-generation pair. The production of a second-generation pair would require 200 settled spat during five years, or an annual production of 40 settled spat.

The biological statistics of a stable *Mya* population appear to be:

3×10^6 eggs/spawning/parent pair
3×10^6 larvae/spawning/parent pair
200 spat must settle during five years
40 spat must settle per year
1 second-generation adult pair produced in five years

Subsequent research may modify these figures and necessitate recalculations, but the principles involved will not be changed.

Mortality

As used here, mortality includes predation and all other causes of death. Calculation of the size of a population after a time, t, during which mortality has taken place involves only the fundamental equation:

$$P_t = P_0 e^{-kt} \qquad (1)$$

in which P_0 and P_t are the initial and final population sizes, e is the base of the natural logarithms, t is time, and k is the coefficient of mortality; when $k = 1$ the population will drop to the $1/e$th fraction per unit of time. The factor e^{-kt} represents the fraction of the population surviving after time t. Substitution of 3×10^6 larvae for P_0, 28 tidal cycles (two weeks) for t, and various values for k, allows calculation of the size of the larva population (resulting from a single spawning pair) which will survive, under various mortality rates, to settle as spat at the end of the 14-day swimming phase. The results of these calculations are shown in Figure 1 and in the $f = 0$ section of Table 1.

Dilution

Dilution is a general term applied by Ketchum, Ayers, and Vaccaro (1952) to all those processes, such as flushing-out to sea or dilution by the addition of extra water, which produce a decrease in population density without any of the population dying. In the situations where *Mya* lives, flushing-out to sea is probably the common mechanism of dilution.

Recent discoveries in coastal oceanography have produced mathematical techniques and field methods which make possible calculation of the effects of dilution. The mathematical techniques were developed by Ketchum (1951) and Ketchum, Ayers, and Vaccaro (1952). The field methods have been developed in large part by these authors and are described in the Appendices of this paper.

The mathematical considerations derive the equation for the effect of dilution:

$$P_t = P_0(1 - f)^t \qquad (2)$$

where P_0 and P_t are the original and final populations remaining in their natal estuary or embayment after time, t (in tidal cycles of 12.4 hours each), during which the population has been subject to intermittent flushing out to sea; and f is the fraction of water lost from the estuary or embayment during one complete tidal cycle, also called the flushing rate. The factor $(1 - f)^t$ represents the fraction retained in the estuary or embayment after time t. The

calculation of f for Barnstable Harbor, Massachusetts is given in Appendix I.

Substitution of 3×10^6 larvae for P_0, 28 tidal cycles for t, and various values between 0 and 1 for f, permits calculation of the size of the larva population (stemming from a single spawning pair) which will remain in the area until they settle as spat at the end of the 14-day swimming stage. The results of these calculations are shown in Figure 1 and in the $k = 0$ portions of Table 1.

Combined Dilution and Mortality

Under estuarine or embayment conditions dilution and mortality proceed simultaneously and produce a greater decrease in population than could be achieved by either process alone. Of the fraction which remains in the area, only a further fraction survives. The equation for combined dilution and mortality is:

$$P_t = P_0(1 - f)^t e^{-kt} \qquad (3)$$

where P_t is the size of the population which *both* survives *and* remains in the spawning area, all other factors as above. Substitution of 3×10^6 larvae for P_0, 28 tidal cycles for t, and letting k vary from 0 to 1.0 at each level of f as f goes from 0 to 0.5 (Table 1) produces a family of curves summarizing the combined effects of dilution and mortality on the larva population, resulting from a single spawning pair, during the two-week swimming phase. The results of these calculations are presented in Table 1 and Figure 2.

RESULTS

Dilution-Mortality Relations of Mya Populations

The production of 40 larvae per year which both remain in the spawning area and survive to settle as spat appears to be the minimum which will allow one parent pair of *Mya* to replace itself, during its period of sexual maturity, with a single pair of second-generation adults, i.e., give a stable local population. More than forty retained and surviving larvae per pair per year represents a population in which there is at least a potentiality for increase. Fewer than forty retained and surviving larvae per pair per year indicates a population which is at least potentially declining.

In the absence of mortality, an estuary or embayment may retain 40 larvae per pair per year to the end of their swimming stage provided the flushing rate does not exceed $f = 0.33$ per tidal cycle (Table 2). In the

TABLE 1

Size of final larva population (from three million fertilized eggs produced by a single spawning pair) both *retained in the spawning area* and *surviving at the end of the 28-tidal-cycle swimming stage as mortality,* k, *varies at various levels of flushing rate,* f.

f	Retention $P_0(1-f)^t$	k	Surviving fraction e^{-kt}	Final population P_t	Harvestable fraction $(P_t - 40)/P_t$
					%
0	3×10^6	0	1.00	3×10^6	99.9
		0.2	37×10^{-4}	1.1×10^4	99.6
		0.4	135×10^{-7}	41	2.5
		0.5	82×10^{-8}	2.5	0
		0.6	50×10^{-9}	0.15	0
		0.8	18×10^{-11}	5.6×10^{-4}	0
		1.0	67×10^{-14}	2.1×10^{-6}	0
0.1	1.6×10^5	0	1.00	1.6×10^5	99.9
		0.2	37×10^{-4}	592	93.1
		0.3	22×10^{-5}	35	0
		0.4	135×10^{-7}	2	0
		0.6	50×10^{-9}	8.0×10^{-3}	0
		0.8	18×10^{-11}	2.9×10^{-5}	0
		1.0	67×10^{-14}	1.1×10^{-7}	0
0.2	5.8×10^3	0	1.00	5.8×10^3	99.3
		0.1	0.0608	353	88.3
		0.2	37×10^{-4}	21	0
		0.4	135×10^{-7}	0.08	0
		0.6	50×10^{-9}	2.9×10^{-4}	0
		0.8	18×10^{-11}	1.04×10^{-6}	0
		1.0	67×10^{-14}	3.9×10^{-9}	0
0.3	138	0	1.00	138	71.0
		0.05	0.2466	34	0
		0.2	37×10^{-4}	0.5	0
		0.4	135×10^{-7}	1.8×10^{-3}	0
		0.6	50×10^{-9}	6.9×10^{-6}	0
		0.8	18×10^{-11}	2.5×10^{-8}	0
		1.0	67×10^{-14}	9.2×10^{-11}	0
0.4	1.84	0	1.00	1.84	0
		0.2	37×10^{-4}	6.8×10^{-3}	0
		0.4	135×10^{-7}	2.5×10^{-5}	0
		0.6	50×10^{-9}	9.2×10^{-8}	0
		0.8	18×10^{-11}	3.3×10^{-10}	0
		1.0	67×10^{-14}	1.2×10^{-12}	0
0.5	0.012	0	1.00	0.012	0
		0.2	37×10^{-4}	4.4×10^{-5}	0
		0.4	135×10^{-7}	1.6×10^{-7}	0
		0.6	50×10^{-9}	6.0×10^{-10}	0
		0.8	18×10^{-11}	2.2×10^{-12}	0
		1.0	67×10^{-14}	8.0×10^{-15}	0

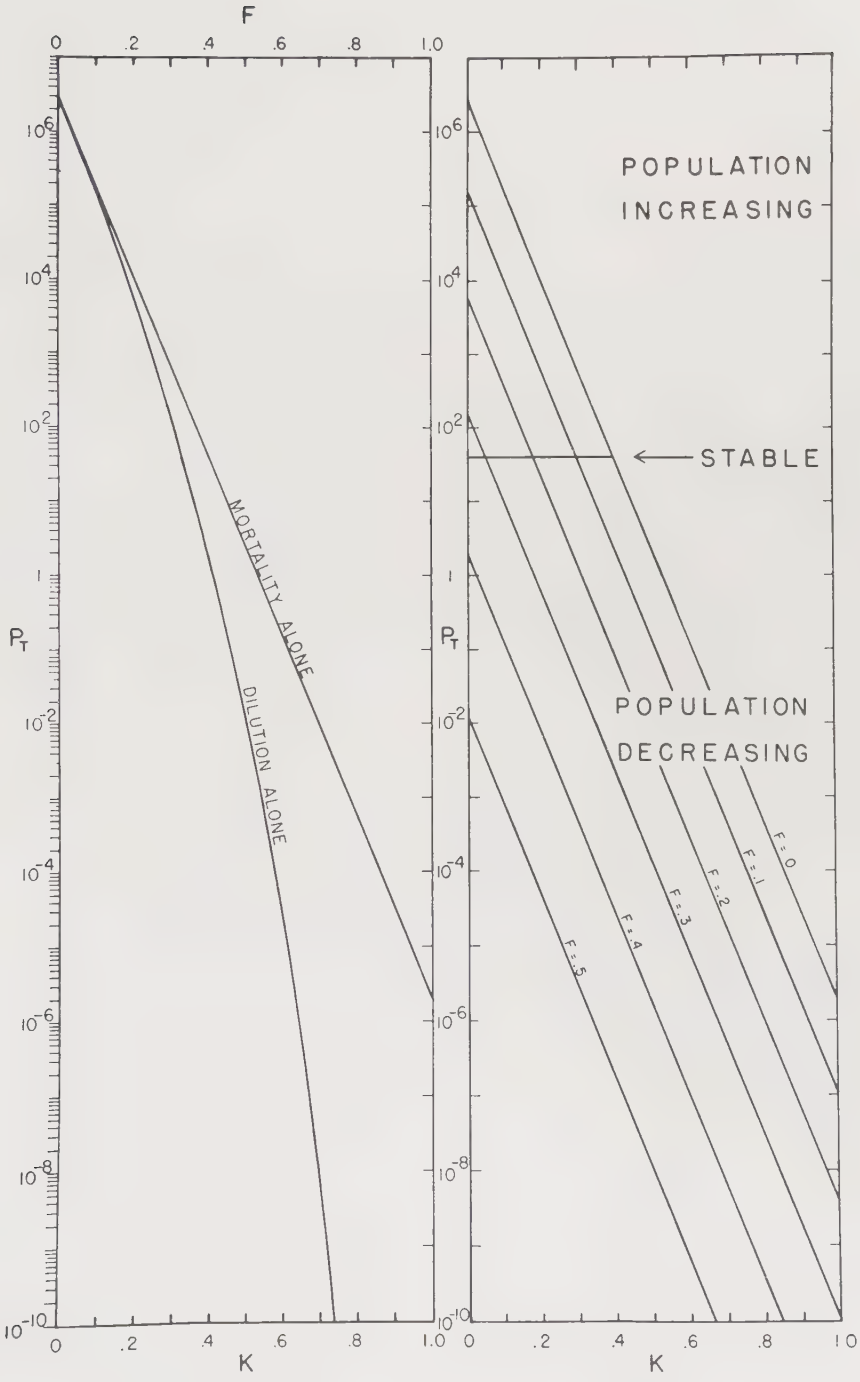

FIG. 1 FIG. 2

FIG. 1. Size of larva population, from a single spawning pair, after 28 tidal cycles at various levels of mortality or dilution alone.

FIG. 2. Size of larva population after 28 tidal cycles as mortality, k, goes from 0 to 1 at flushing rates, f, of 0 to 0.5. The 40 spat/pair/year level of a stable local population is indicated.

TABLE 2. *Relations of* f *and* k *at the 40 Spat/Pair/year level*

f	*k*
0.33	0
0.30	0.044
0.20	0.18
0.10	0.30
0	0.41

absence of dilution, 40 larvae per pair per year may survive in the estuary or embayment if the coefficient of mortality does not exceed 0.41 per tidal cycle.

Suitable Locations for Mya Culture

The primary criterion for the selection of localities suited to the cultivation of *Mya* appears to be that both the flushing rate and the coefficient of mortality must be low. The calculations summarized in Figure 2 and Table 2 indicate that a stable population is possible between $f = 0.33$, $k = 0$ and $f = 0$, $k = 0.41$.

The Harvestable Fraction

The characteristics of a stable *Mya* population indicate that an annual production of 40 retained and surviving larvae (spat) per parent pair is adequate for maintenance of the population. Any excess over 40 spat/pair/year would produce second-generation adults in excess of those needed to maintain the population. Since the 1%-survival factor for spat will cancel in numerator and denominator, the harvestable fraction of the second-generation adults would be:

$$\frac{(P_t - 40)}{P_t} = \text{harvestable fraction.} \quad (4)$$

This shows that the ratio may be determined from the final larva population as calculated from the local flushing rate and local mortality coefficient. Further, the excess reproductive potential of each parent pair is represented by:

$$\frac{(P_t - 40)/3 \times 10^6 \text{ larvae/pair}}{P_t/3 \times 10^6 \text{ larvae/pair}} \quad (5)$$

$$= \text{excess reproductive potential/pair}$$

and the excess reproductive potential of the parent population is represented by:

$$\frac{N\,(P_t - 40)/3 \times 10^6\, N}{N\,P_t/3 \times 10^6\, N} \quad (6)$$

$$= \text{excess reproductive potential of population}$$

where N is the number of spawning parent pairs. Cancellation of common factors in both equations (5) and (6) again indicates that the significant matter is the ratio of the excess larvae to the total larva population, and that the harvestable fraction of the parent stock can be calculated from the number of eggs/pair, the local flushing rate, and the local mortality coefficient.

It is also possible to calculate the number of harvestable adults in the parent stock but this is a less directly usable result than the percentage harvestable, for shellfish populations are estimated in bushels per acre or similar units and are managed by opening or closing various areas of bottom to digging.

DISCUSSION

Possibly the most-needed data in the field of *Mya* culture are determinations of the mortality coefficient. Data of this kind are nearly non-existent. Table 1 repeatedly indicates that a small difference in mortality can change the harvestable fraction from zero to a major portion of the population. From this it is evident that direct determinations of mortality must be very carefully done if usable data are to be obtained.

Additional studies on the survival of settled *Mya* spat are needed to test the validity of the 1% survival rate used here.

Practical tests of the accuracy of the harvestable fraction as a prediction of the portion of the breeding stock to be harvested are also needed.

We need field observations of the distribution of larvae in estuaries having a net seaward flow of freshwater in the upper layers and net landward movement of salt water along the bottom. The computations will treat the populations of such localities as though they remained in the upper layers throughout the larval period. Actually, the

larvae approach the bottom prior to settling out as spat. This would bring them into the salt water inflow and result in their being returned to the estuary, as Bousfield (1954) has observed in the case of late barnacle larvae. Late larvae settling into the salt water inflow would result in the final population of the estuary being higher than the computations would predict.

Applications of the Method

The flushing times and flushing rates of several estuaries and embayments have been determined; the flushing rate curves for two estuaries (Raritan Bay, New Jersey, and Great Pond, Falmouth, Mass.) where the author personally knows *Mya* stocks to be persistent have been entered in Figure 3. Lack of data on mortality coefficients in these localities prevents their being characterized by points rather than by lines.

The harbor of Barnstable, Massachusetts, is a fairly typical tidal embayment; in it occasional small populations of *Mya* appear but do not survive. By the method described in Appendix I, the author has calculated the flushing time of Barnstable Harbor to be 5 tidal cycles, i.e., the flushing *rate* is 0.2 per tidal cycle.

The author has enough data on *Mya* larvae in Barnstable Harbor to calculate one single mortality coefficient. At mid-ebb on 13 August 1947 beside Phillis Island in the mid-length of the harbor there were an average of 33.8 straight-hinge-stage *Mya* larvae per liter of water. Two tidal cycles later at mid-ebb on 14 August 1947 at the same place there was an average of 3.1 straight-hinge-stage *Mya* larvae per liter of water. The decrease of larvae during this one-day period is attributable to the combined effects of dilution and mortality. Substitution into Equation (3) of 33.8 larvae per liter for P_0, 3.1 larvae per liter for P_t, 0.2 per tidal cycle for f, and 2 tidal cycles for t allows the calculation of the coefficient of mortality, k:

$$\begin{aligned} P_t &= P_0(1-f)^t e^{-kt} \\ 3.1 &= 33.8(0.8)^2 e^{-2k} \\ k &= 0.97 \end{aligned}$$

In waters with a flushing rate of 0.2 the indicated maximum coefficient of mortality

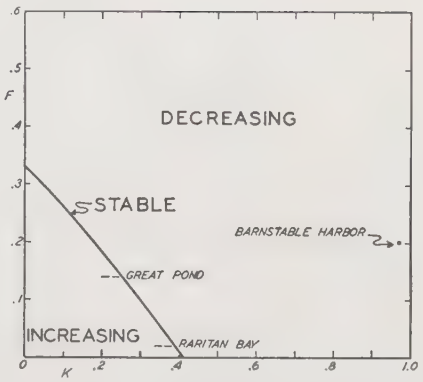

FIG. 3. The 40 spat/pair/year stable population level in relation to flushing rate, f, and mortality coefficient, k. The flushing rates (dashed lines) of Raritan Bay and Great Pond, which have persistant *Mya* populations, and the point $f = 0.2$, $k = 0.97$ representing Barnstable Harbor, without a persistent *Mya* population, are indicated.

which will allow a stable population is 0.18 (Table 2 and Fig. 2). Thus, on the basis of the one single determination possible, Barnstable Harbor appears to have a natural coefficient of mortality five times greater than the maximum which will allow a stable population from local reproduction alone. This argues that Barnstable Harbor is a locality in which reproduction of local stocks is unable to maintain a stable local population (see Fig. 3).

The history of the harbor is not in disagreement with this conclusion and certain facets of its history independently point to the same general conclusion.

From earliest records until the economic depression of 1929, Barnstable Harbor had a history of an abundant *Mya* population, with huge augmentation by enormous sets of spat occurring at irregular intervals of a few years. Between these huge sets the population in the harbor appears to have declined gradually. Huge recruitment at irregular periods of more than one year suggests influx of swarms of spat, just ready to settle, from some area outside the harbor.

Investigation of the oceanography of Cape Cod Bay confirms this suggestion. Drift bottle studies by Bigelow (1927) show that the alongshore currents of Cape Cod Bay move in a counterclockwise direction with an average speed of 1.9 nautical miles per day. *Mya* larvae entering Barnstable Harbor

as spat just ready to settle at the end of a 14-day drift in this current must have traveled 26.6 nautical miles. Retracing the curving path of the current for 26.6 miles brings one to the harbor of Plymouth, Massachusetts. It thus seems both possible and probable that the occasional enormous *Mya* sets formerly received by Barnstable Harbor were larvae produced in Plymouth Harbor, which under occasional unusually fortuitous conditions were able to complete the journey to Barnstable. Such fortuitous sets, indeed, appear to have been the only significant recruitment to the harbor's *Mya* population.

The observed effects of the economic depression of 1929 in no way disagree with these conclusions. During the depression clamming afforded the only livelihood available to many of the people of both Plymouth and Barnstable. The *Mya* stocks of both harbors were heavily depleted during this period, and Barnstable then gradually lost the remainder of its population.

Since the heavy digging-out of the harbors' stocks during the depression, the enormous sets that Barnstable formerly received have been virtually absent; a moderate set in 1941 survived, grew, and supported a commercial clamming industry through 1947; a set in 1946 did not survive, nor did a small set in 1951. Failure of these sets to survive has been shown by Turner *et al* (1948–1951) to be due to the harbor's normally-large predator populations, which lead a marginal existence in the absence of clams and which seek out and completely destroy any small sets. A set sufficient to repopulate Barnstable Harbor must be so large that it can support the predators and still have a residue surviving to maturity. The history of the *Mya* populations of Barnstable and Plymouth is reviewed in detail by Turner *et al* (op. cit.).

SUMMARY

From currently accepted information on the spawning and survival of *Mya arenaria* it is calculated that stable populations can be maintained if each pair of spawning adults produces an annual average of 40 spat which *both* survive *and* remain in the spawning area. Populations would tend to increase if more than 40 such spat per pair per year are produced, to decrease if production is less than 40.

The sizes of larva populations (from a single pair of spawners) which both survive and remain in the spawning locality until spatfall, under various conditions of flushing rate and mortality, are calculated. The graph of these results expresses the overall relationship between flushing rate, mortality, and size of larva population retained in the area and surviving until spatfall. The position at which the level of 40 spat per pair per year falls across this overall relationship provides a criterion for judging whether an existing adult population is potentially increasing, stable, or decreasing under the conditions of flushing rate and mortality which prevail.

Field measurements of flushing rate and mortality may be compared to the overall relationship as a means of estimating the suitability of essentially *Mya*-less localities as places for the cultivation of the shellfish.

A formula for estimating the harvestable fraction of the existing population (under local flushing rate and mortality conditions) has been derived.

Additional determinations of natural coefficients of *Mya*-larva mortality, of survival from spatfall to maturity, of egg production per spawning pair, and field tests of the method as a whole, are needed for the refinement of the method; it is not anticipated that these will modify the underlying principles.

The method, combined with the local oceanography, adequately explains the recorded history of *Mya* production in Barnstable Harbor, Massachusetts.

APPENDIX I

The flushing time is defined as the average number of tidal cycles required for the total freshwater inflow (see Appendix II) to replace the quantity of freshwater which is present in an estuary or embayment at any high water during constant runoff conditions. It is determined by computing the volume of freshwater in the area at high water, dividing by the volume of total freshwater inflow per tidal cycle to obtain the flushing time. The reciprocal of the flushing time is the flushing rate, f.

In small estuaries or tidal embayments where there is no *vertical* gradient in salinity (although

TABLE 3

Freshwater accumulation in Barnstable Harbor, high water, 29 August 1947

No vertical salinity gradient. Base salinity = greatest salinity = 31.64 ‰. Fresh water fraction = (base salinity minus inter-contour average salinity)/base salinity

Salinity		Area	Average depth, ft	Volume	Freshwater fraction	Freshwater volume, ft^3
Range	Average	ft^2		ft^3		
31.60–31.50	31.55	58.7×10^6	15	880×10^6	0.003	2.6×10^6
31.50–31.02	31.26	37.2×10^6	10	372×10^6	0.012	4.4×10^6
Total freshwater accumulation						7.0×10^6

an extensive horizontal gradient may exist along the length of the area), the areas between adjacent salinity contours (drawn on navigation charts) are determined by planimetry and each area is multiplied by the average of all the depth soundings it encloses; an inter-contour volume is thus obtained for each area. Each inter-contour volume is multiplied by the freshwater fraction (see Table 3) represented by its average salinity to obtain the inter-contour volume of freshwater. Summation of these freshwater volumes gives the total freshwater volume; this is divided by the total freshwater inflow per tidal cycle to give the flushing time.

This method has been used in Barnstable Harbor; the results are shown in Table 3.

The average flushing time of Barnstable Harbor is, then,

$$\frac{7.0 \times 10^6 \text{ ft}^3 \text{ accumulated freshwater}}{1.4 \times 10^6 \text{ ft}^3 \text{ total inflow/tidal cycle (Appendix II)}} = 5.0 \text{ tidal cycles}$$

and the flushing rate is 0.2 per tidal cycle. Ketchum (1954) using a different method, has estimated Barnstable's flushing rate to be 0.3.

APPENDIX II

In sandy soils ground-water seepage contributes freshwater which cannot be measured directly. This acquisition is apt to be a significant part of the total freshwater inflow in tidal embayments (characterized by the absence of a river; runoff entering from small streams) and less so in estuaries (characterized by the presence of a river whose flow usually constitutes the major part of the freshwater inflow). Measurements of stream runoff and water transports into and out of Barnstable Harbor in August 1948 during a period of low rainfall comparable to that of August 1947 allow an analysis of the hydrology of the area.

The Barnstable watershed acquired from a 0.14 inch rainfall on 30 August 1948:

$$22.8 \text{ mi}^2 \text{ watershed} \times 5280 \text{ ft}^2/\text{mi}^2 \times \frac{.011 \text{ ft rain/day}}{2 \text{ tidal cycles/day}} = 3.4 \times 10^6 \text{ ft}^3/\text{tidal cycle.}$$

After the rainfall, measured stream flow was only 0.3×10^6 ft^3/tidal cycle and the net transport seaward through the harbor mouth was 1.4×10^6 ft^3 of freshwater/tidal cycle. The latter was determined from a series of stations across the harbor mouth which were occupied at each hour of the tidal cycle; at each station surface, mid-depth, and bottom current velocities and salinity samples were obtained. From the hourly areas of the section, the hourly current velocities, and the hourly freshwater fractions, the total inward and outward transports of freshwater were determined. The excess of ebb-tide freshwater outflow over flood-tide return of freshwater represents the sum of runoff and groundwater seepage.

The results may be summarized as follows:

	(all $\times 10^6$ ft^3/tidal cycle)	
Rainfall		3.4
Transport seaward (runoff plus seepage)	1.4	
Subtract runoff	0.3	
Seepage	1.1	
Runoff plus seepage		1.4
Evaporation, interception, soil-retention and retention in harbor (by difference)		2.0

Since inflow of freshwater by seepage is as effective in displacing the accumulated freshwater of the harbor as is runoff via streams, the sum of the two must be used as the total freshwater inflow in the determination of the flushing time—from which flushing rate is obtained.

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Deep Standing Internal Waves in California Basins[1]

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ABSTRACT

Periodic variations of the water temperature observed at depths of 700, 850, and 1000 m in the Catalina Basin (sill at 982 m, bottom at 1357 m) lead to the inferred existence of deep standing internal waves having an amplitude of 130 to 200 m. The presence of such waves may account for the prior observation of bottom currents as great as 18 cm/sec, of suspended sediment near the basin floors, of a virtual absence of gradients of oxygen and nutrients near the bottom, of locally coarser sediments at basin sills than at their bottoms, and of replacement of basin water so rapidly that oxygen does not become deficient nor do regenerated nutrients become abnormally concentrated in the basin waters.

INTRODUCTION

During 1938 and 1939 measurements of currents were made near the ocean bottom of southern California in such environments as shelves, bank tops, slopes, submarine canyons, and basin floors (Revelle and Shepard 1943, Shepard 1948). Three Ekman current meters were suspended in a tripod frame at heights of 20, 48, and 84 cm above the bottom with a tripping mechanism so arranged that the meters would begin recording velocity and direction of the current when the tripod was set on the bottom and would stop recording when it was hoisted. Among the unexpected results obtained with this equipment were velocities of more than 10 cm/sec (0.2 knot) in two basins, at a point 800 m below the sill depth of one, Santa Cruz Basin (Figs. 1 and 2). At the time, the currents were thought to be due to movements of water in eddies having vertical axes (Shepard, Revelle, and Dietz 1939).

No further studies of basin floor currents were made until 1951 and 1952 when photographs taken with the benthograph (Emery 1952) showed the presence of larger numbers of light scattering particles in water within 10 or 20 m of the floors of the basins than higher above the bottom, suggesting a slight stirring of sediment by turbulent bottom currents. This interpretation was supported by the later discovery by Rittenberg, Emery, and Orr (1955) that concentration gradients of oxygen and nutrients are restricted to the bottom 0.5 m layer of water and that samples of water between 0.5 and 5 m above the bottom contained the same concentrations of oxygen and nutrients as the main mass of basin water. This distribution was interpreted as indicating that turbulent mixing of oxygen and nutrients in bottom waters occurs at a rate that is rapid compared to their use or regeneration in bottom sediments.

Grain-size analyses of sediments show that the basins are floored by sediment consisting mostly of clay and silt particles (Emery and Rittenberg 1952, Emery 1954a). Neighboring banks and shelves are covered by sands composed of broken shells, Foraminifera, glauconite, and residual rock fragments; clay and silt particles are subordinate owing to the winnowing action of waves and currents. At the sills of basins most of the sediment samples (Table 1) are clays and silts nearly as fine as those of the basin floors, but some are sands consisting of Foraminfera, glauconite, and rock fragments. As pointed out by Revelle and Shepard (1939), there is little uniformity between cores taken in the same sill or even between samples at different depths in the same core. The presence of sands within some sills indicates that currents at the sills are strong enough to prevent deposition of clays and silts. The fact that most of the sediments are only slightly coarser than

[1] Allan Hancock Foundation Contribution No. 173.

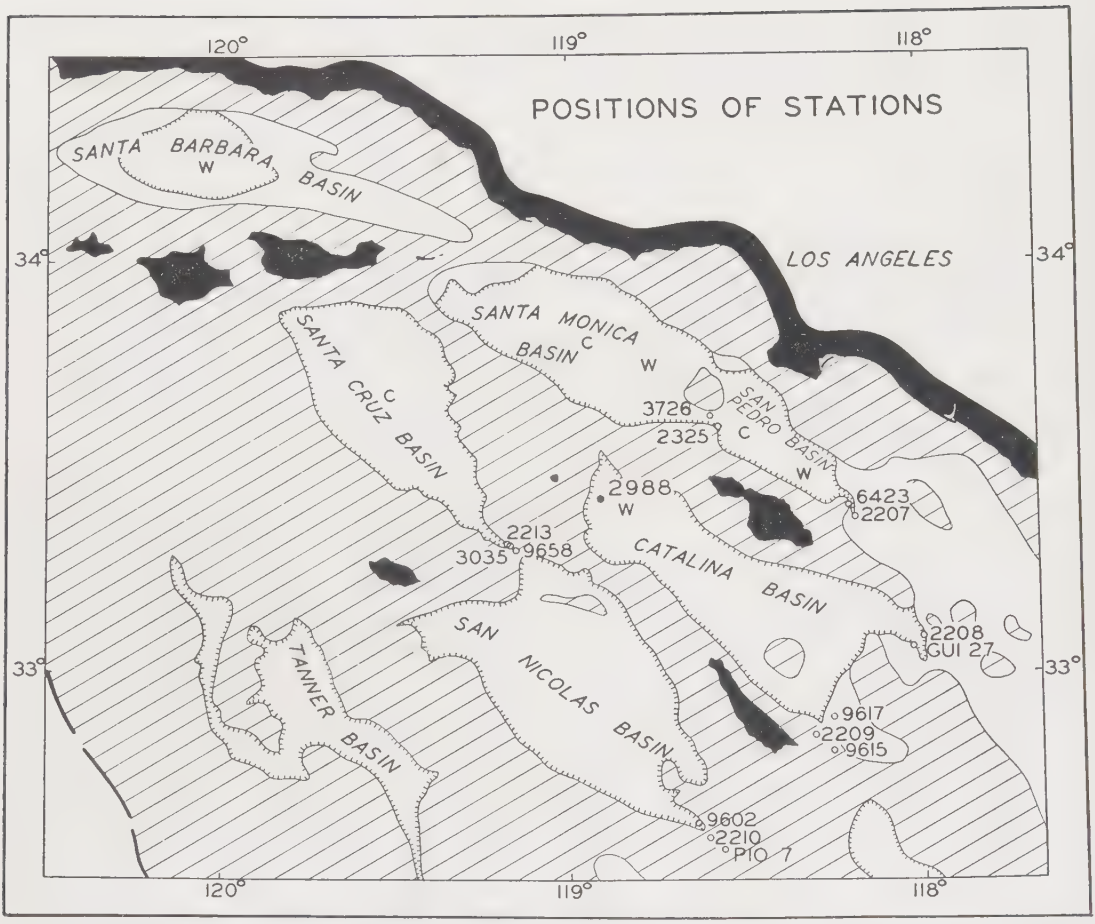

FIG. 1. Basins off southern California. Hachured lines indicate outlines of closed portions of basins; plain white pattern shows deep flat areas above sill depth of basins; cross-hatching shows non-basin areas; *C* marks positions of current meter stations; *W* marks positions of stations where chemistry of bottom water was studied; small circles are stations where sediment samples were collected at or near the basin sills (2000 and 3000 series are samples by University of Southern California; 6000 and 9000 series by Scripps Institution—Garrison and Takasaki 1950; GUI and PIO are by Coast and Geodetic Survey vessels).

average basin floor sediment suggests that the strong currents are very local in distribution. Because of the great depth the currents cannot be the result of surface wind waves; the local distribution of the coarse sediment within the sills suggests that the currents may represent a type of funnelling of water into or out of the basins.

Studies of water temperatures within and above the centers of the basins (Emery 1954b) showed that the water is nearly uniform in temperature and salinity between the sill depth and the bottom depth and is of the same temperature and salinity as water of the open sea at a depth corresponding to that of the basin sills. Thus, it is evident that the basins are filled with water of the open sea from a depth approximately equal to that of the sills. Considerations of the oxygen and nitrate budgets showed that the water of one basin (Santa Barbara) must be completely replaced from the open sea in a period of less than 2 and less than 20 years, respectively (Rittenberg, Emery, and Orr 1955). Later more precise data on the rate of deposition of sediments (based on carbon-14 ages) require the rates to be revised to 5 and 50 years, respectively.

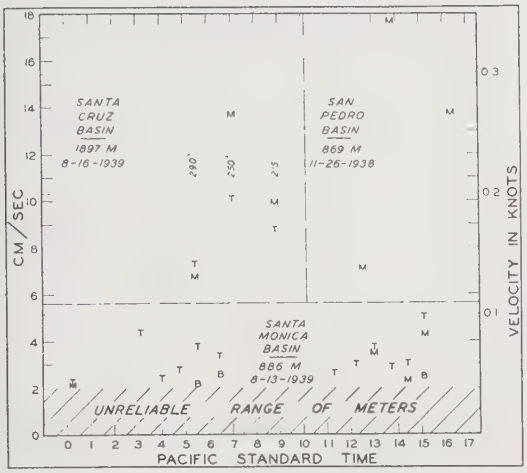

FIG. 2. Current meter measurements at basin floors made in 1938 and 1939 by Revelle and Shepard—taken from Shepard's field notes. *T*, *M*, and *B* refer to current velocities at 84, 48, and 20 cm above the bottom, respectively. Direction of current, given in degrees of true azimuth, was measured only in Santa Cruz Basin.

In summary, the background data consists of measured currents as great as 18 cm/sec near the centers of basins, inferred currents to account for a concentration of suspended particles in bottom water and for the absence of concentration gradients of oxygen and nutrients in bottom water, locally coarser sediment in basin sills, and a complete replacement of basin water within only a few decades. All of these facts show that movement of basin water occurs, but none of them defines the kind of movement.

A hint of the kind of movement was provided by the fact that measurements repeated at irregular intervals up to 22 years detected small variations in the temperature of waters above some basins (at depths shallower than their sills), but none in the nearly uniform water deeper than sill depth. These variations suggested the possible presence of a deep standing internal wave, whereby the deep basin waters may oscillate back and forth alternately lifting and dropping the overlying mass of water. A special trip of VELERO IV was arranged in order to check this possibility by frequently repeated temperature series at one end of a basin.

TABLE 1. *Median diameters of sediments*

Basin	Floor* Average μ	Sill	
		μ	Station
San Pedro	6.6	7.2	6423
		8.9	2207
Santa Barbara	4.5		
Santa Monica	5.3	25	2325
		7.6	3726
Santa Cruz	5.2	3.4	9658
		5.6	2213
		6.8	3035
Catalina	3.9	3.3	9615
		3.7	GUI 27
		5.2	2208
		35	9617
		120	2209
San Nicolas	2.6	17	PIO 7
		130	2210
		225	9602

* Analyses of basin floor samples from Emery and Rittenberg (1952) neglecting sand layers.

METHOD

A station (AHF 2988) was positioned at one end of Catalina Basin, a basin that is 85 km long, 19 to 45 km wide, 1357 m deep, with a sill at 982 m. The depth at the station was 1300 m. Islands occur along both sides and at one end of the basin; a shallow bank forms the other end. The deeper parts of the rim are at the corners of the basin (Fig. 1). More detailed topography of the area is given by maps of Shepard and Emery (1941).

For each temperature series the ship was returned to the same station position, using visual bearings and radar ranges as control. Wire angles at the surface during the study were mostly less than 5° from the vertical and exceeded 12° for only two measurements. Because of the usual decrease of wire angle with depth, there was found to be no correlation of measured temperatures with wire angle.

Twenty lowerings of three Nansen bottles each equipped with two protected reversing thermometers were made at one- or two-hour intervals during a period of 25 hours to

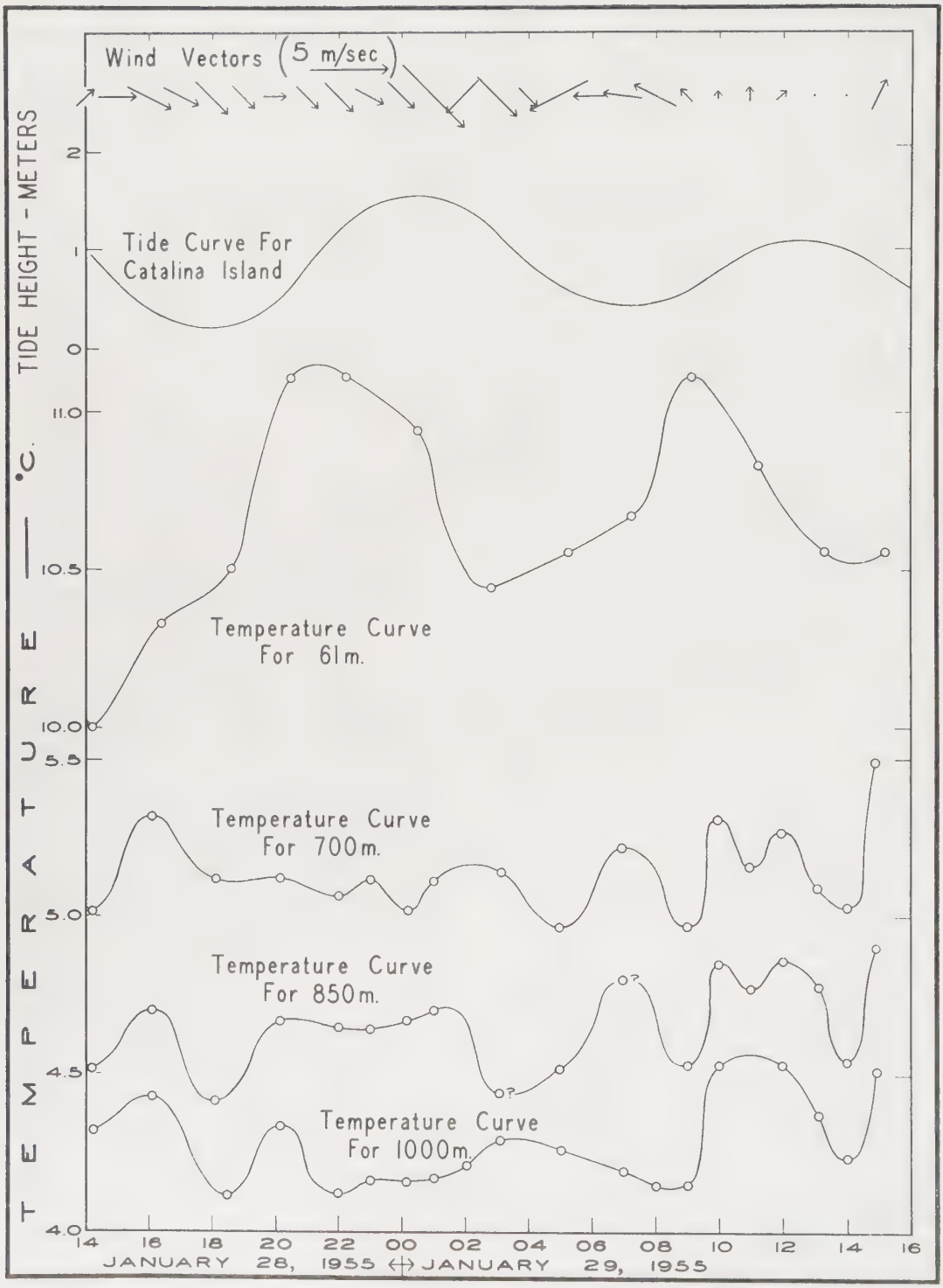

FIG. 3. Variation of temperature at 61, 700, 850, and 1000 meters during a 25-hour period near west end of Catalina Basin (Station 2988).

TABLE 2. *Maximum wind at San Nicolas Island between 0630 and 1630 daily*

January	Direction	m/sec	
16	NW	15.0	
17	NW	7.5	
18	S	13.0	
19	NW	7.5	
20	NW	8.5	
21	NNE	4.0	
22	NNW	6.0	
23		<2.5	
24	WNW	8.0	
25	NW	5.0	
26	NE	4.0	
27	NW	3.5	
28	NW	3.5	Dates of study
29	SSE	4.0	Dates of study
30	S	5.5	

depths of 700, 850, and 1000 m, respectively. On two lowerings one or two bottles obviously malfunctioned and the results were discarded. On the other lowerings the corrected readings of each pair of thermometers agreed to within a mean difference of 0.02°C and a maximum difference of 0.05°C, after adjustment for systematic differences. On two observations, indicated by question marks on Figure 3, one thermometer of a pair failed to work. During the lowering of reversing thermometers a temperature-depth curve between the surface and 61 m was obtained with a bathythermograph.

Wind velocity and direction were recorded aboard ship. The wind was very light, never exceeding 6 m/sec and usually being less than 2 m/sec, in contrast to the winds of a week or two before that reached 15 m/sec (Table 2). The tide curve, taken from Coast and Geodetic Survey predicted tables for Catalina Island (Fig. 3), differed by less than 10 cm from the observed tide curve at Los Angeles Harbor.

RESULTS

The measurements showed a variation in water temperature during the 25-hour period of 1.2°C at 61 m, 0.52°C at 750 m, 0.48°C at 850 m, and 0.41°C at 1000 m (Figs. 3 and 4). The temperature variation even at 1000 m is more than 20 times those found below sill depths at stations near the middles of several basins (Santa Barbara, Santa Cruz, San Pedro, and San Nicolas) that were reoccupied at intervals of a year or more (Emery 1954b). Expressed in terms of depth, the variations of temperature amount to 130 m vertical movement of the 5°C isotherm (Fig. 5) and nearly 200 m for the 4.5°C isotherm.

The temperature curve at 61 m clearly has a tidal period, being greatest about two hours after low tide. Two or more periods are indicated for the deeper temperatures: one of the order of two hours and another of the order of eighteen hours. It is difficult to believe that the temperature variations at depth could be produced by uniform raising and lowering of whole isothermal surfaces throughout the basin because enormous volumes of water would have to be introduced and expelled from the basin in short periods of time. A more reasonable explanation is that one or more deep stand-

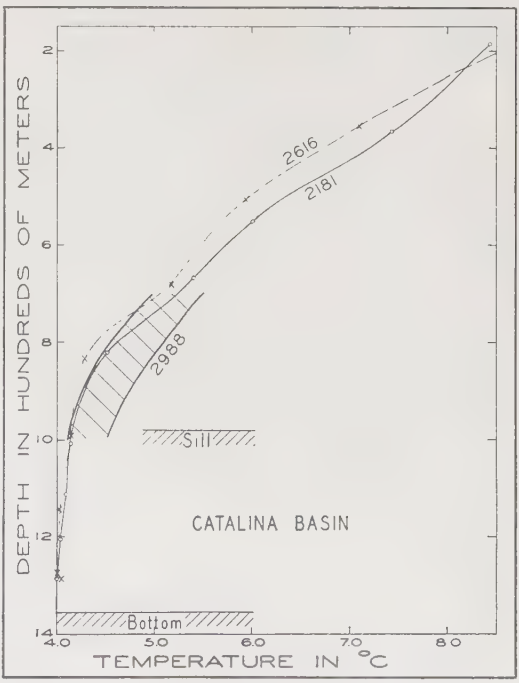

FIG. 4. Temperature-depth measurements for Catalina Basin showing range of temperatures above sill depth during the 25-hour study of 28 and 29 January 1955 (Station 2988—cross-hatching). The data of 8 November 1952 (Station 2181 at *W* of Figure 1—circles) and of 31 March 1954 (Station 2616 at same position—crosses) show the characteristics of the temperature-depth curve at other depths.

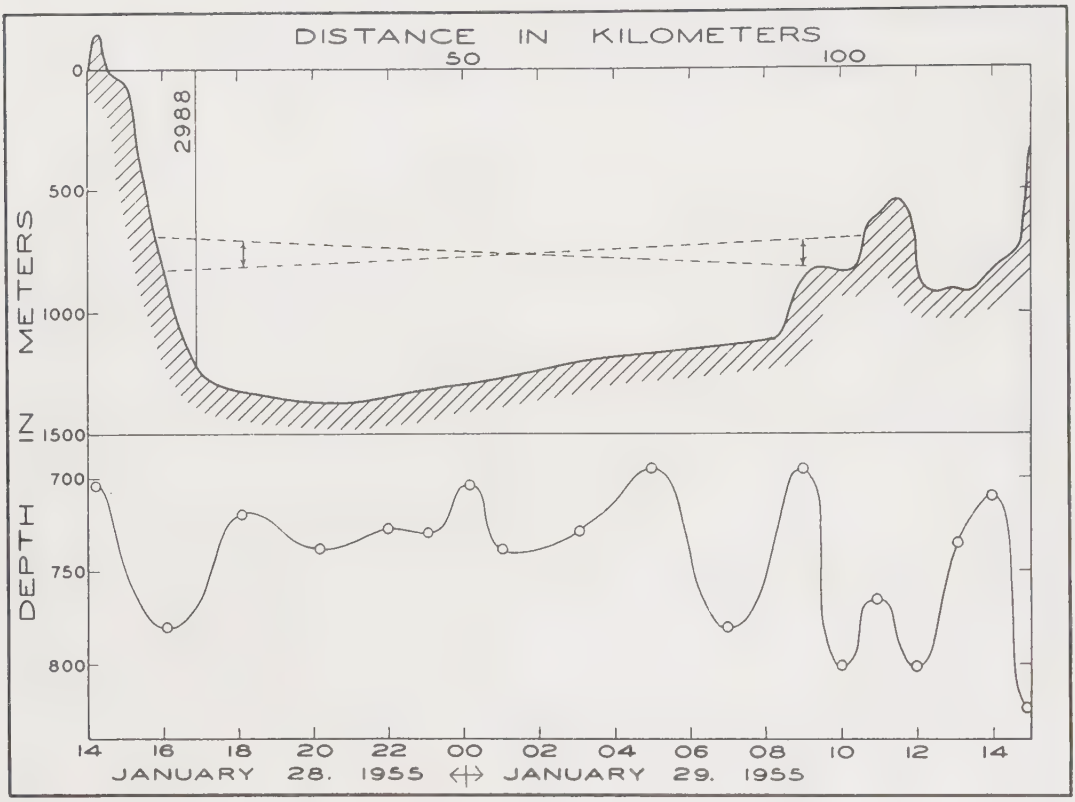

FIG. 5. *Top.* Longitudinal profile of Catalina Basin from Santa Barbara Island on left to edge of Fortymile Bank on right. Dash lines show inferred possible oscillation of 5°C isotherm along length of basin. *Bottom.* Depth variation of 5°C isotherm at Station 2988 on 28 and 29 January 1955 as interpolated from curves of temperature variation shown by Figure 3.

ing internal waves are present. The simplest such wave would be one having a node near the middle of the basin (Fig. 5) but present data do not rule out the possibility of there being several nodes or of waves transverse to the basin's length. If the water oscillates as a deep standing internal wave having antinodes at the ends of the basin, little or no water should enter or leave the basin during the oscillation. Under such conditions the currents at the sill may be only slightly greater than the velocities required to replenish the basin water in the computed period of 5 to 50 years.

Standing internal waves at the thermocline of lakes have previously been studied by Mortimer (1951) and others, and similar waves in fjords have been observed (Sverdrup, Johnson, and Fleming 1942: 600–601). In the Gulf of California Sverdrup (1940) and Munk (1941) showed the presence of deep standing internal waves having an amplitude of about 100 m. In several of these studies a close correlation was shown to exist between the observed period of oscillation and that computed from the dimensions of the basins and the density distribution of the waters. Before there can be much success in such a study of Catalina Basin a method must be devised for measuring temperature changes at great depth at shorter time intervals than are permitted by the use of reversing thermometers. Perhaps the greatest success might result from lowering of thermistor beads or other electrical devices which can make continuous records on deck.

For the present it appears evident that periodic vertical movements of deep water of Catalina Basin produce the bottom currents that stir the bottom sediment and nearly obliterate bottom gradients of nutrients and

oxygen. The large movements probably also aid in mixing of basin water with lighter overlying water, leading to eventual complete replacement of basin water by new water flowing across the basin sill. This flow not only winnows the sediment at the basin sill but also replenishes the oxygen in the basin, thus accounting for the absence of stagnant water in any of the basins off southern California.

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The "Stress-drop Jet" in Lake Mendota

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ABSTRACT

Under certain conditions a rapid increase of current velocity is observed at the bottom of the epilimnion. This phenomenon seems to be associated with a rapid decrease of wind stress on the lake surface. It is postulated that the energy for this "jet" is stored in the solenoid field set up by the preceding wind. It must then represent the first swing of an internal seiche.

INTRODUCTION

During the Great Plains Field Expedition sponsored by the Geophysical Research Division of the Air Force Cambridge Research Center in the summer of 1953, a new and unusual wind phenomenon was discovered. When the surface wind stress dropped (on certain occasions) due to stabilization in the evening, a layer of high velocity winds developed at the top of the friction layer. This was followed by the development of strong winds to the right of the original "jet" with a delay of the peak velocities amounting to four or five hours. This turning to the right in a quarter of a pendulum day, plus theoretical considerations, has led Blackadar (1955) and Lettau (1955) to the conclusion that this "low level jet phenomenon" is a variety of inertial oscillation.

It would be reasonable to assume that if a drop in surface stress were to produce a "jet" at the top of the friction layer in the air, then a "jet" should also appear at the bottom of the friction layer in a lake, i.e. at the thermocline. The authors therefore examined the Lake Mendota current data for evidence of such a "jet". This was done under the auspices of the Lakes and Streams Investigations Committee and with a grant by the Research Committee of the University of Wisconsin.

DATA

Since even the downwind currents in a body of water are upwind relative to the overlying surface of the air, the *relative* velocities increase as depth increases within the friction layer in the water just as they do as height increases in the air. As the surface stress decreases, the relative speed of both air and water should decrease, but if the analogy of water and air is valid, then as the velocity at the top of the air friction layer increases, the reversed velocity at the bottom of the water friction layer should also increase.

The first observation of this effect was made on 20 July 1954. On this occasion, the wind during the day had been between 3 and 5 cm/sec and the currents at 1 and 2 meters depth had been about 8 cm/sec, while at 5 meters, just over the thermocline, the current had been about 2.5 cm/sec. At the time of stabilization, late in the afternoon, the wind shifted and dropped so that the down-current component of the wind nearly disappeared. Shortly thereafter, the currents reversed direction and the distribution of velocity changed so that the currents at one and two meters dropped to 2–3 cm/sec and the five meter current increased to 6–10 cm/sec.

On 23 July 1954, the wind current pattern during the day was similar to what it had been on the 20th. However, no notable change of wind occurred in the late afternoon, and the evening cruise of that day showed no rearrangement of current pattern.

On the 18th of August, the winds during the day had been 5–7 m/sec, sufficient to preclude any stratification within the epilimnion such as had existed on the 20th and 23rd of July. Late afternoon stabilization associated with a shift and decrease of wind velocity occurred on this date as it had on July 20. Associated with the rapid drop

FIG. 1. Time variation of currents off Second Point, Lake Mendota, during the night of 20–21 August 1954. The graphs show the magnitude of the currents at the indicated depths; the vectors denote the wind velocity with a south wind pointing towards the top of the figure. *NM* indicates not measurable.

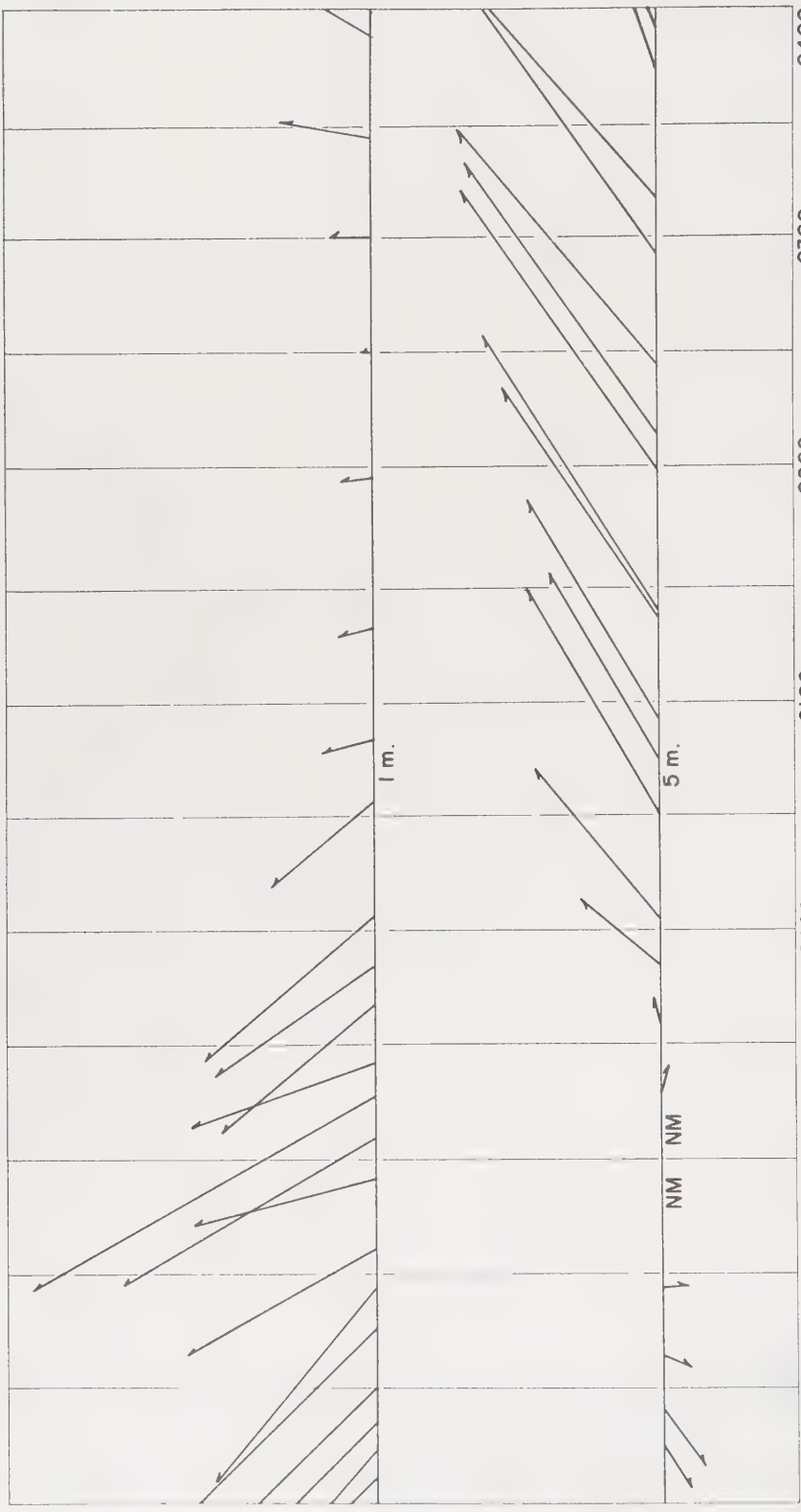

FIG. 2. Time variation of current vectors at the same place and time as Fig. 1 showing the reversal of the 5-m current associated with the drop of wind stress just before midnight. The 5-m current in this area is frequently 90 degrees to the left of the upper currents when the wind is actively driving the circulation.

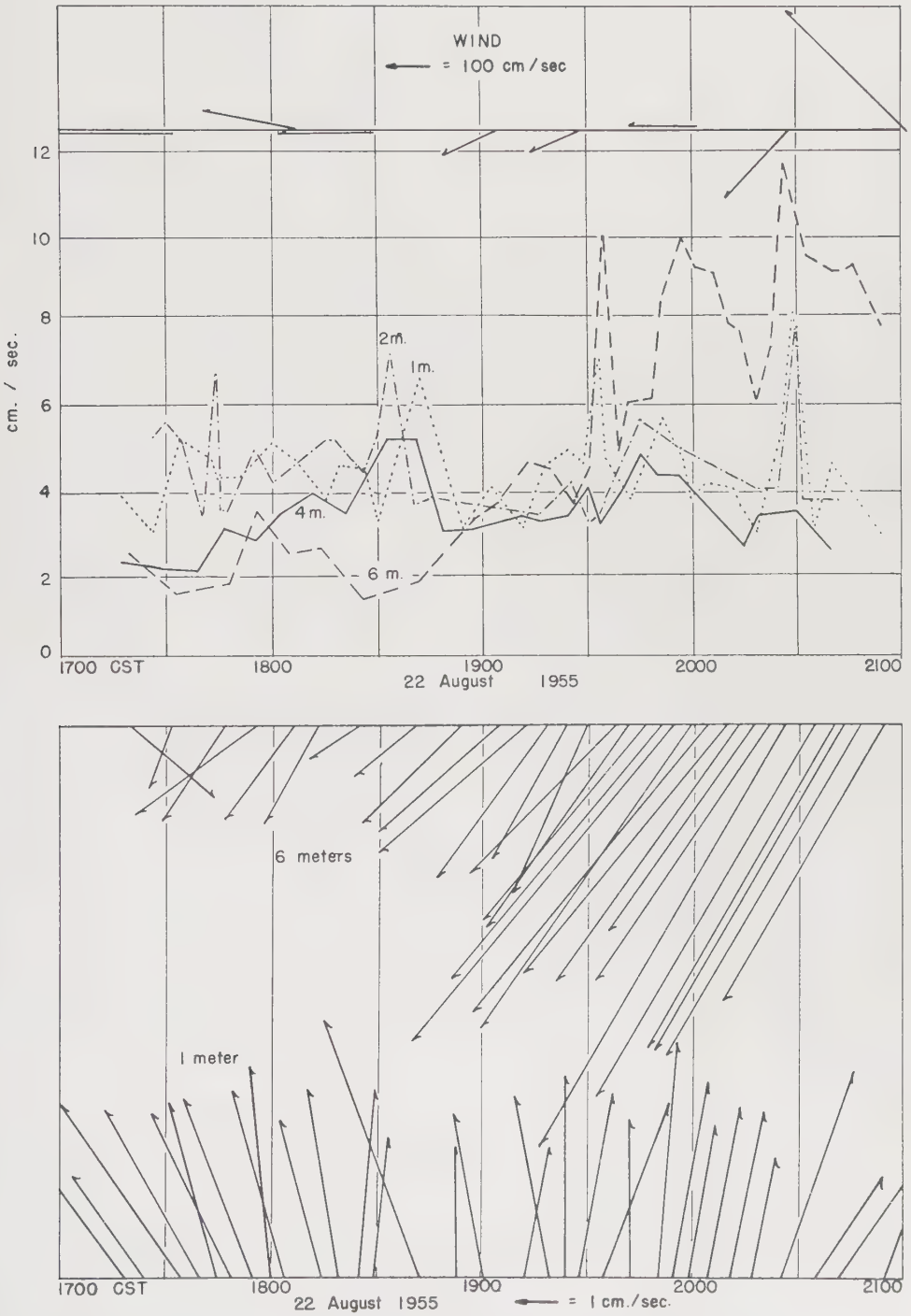

FIG. 3. Time variation of currents off Picnic Point, Lake Mendota, on 22 August 1955. Conventions as in Figs. 1 and 2. On this occasion while the wind did not disappear entirely, the downcurrent component did vanish. Certain differences between Figs. 1 and 3 are due to the locale of the observation.

of down-current wind velocity, the currents at shallow depths decreased from 10–16 cm/sec to 2–5 cm/sec and shifted about 90 degrees to the right, but at 5 m depth the current decreased only 2–4 cm/sec to a value of 1–4 cm/sec with no appreciable change in direction. Bathythermograph drops on the first two dates had shown a gradient of 1–2°C in five meters as opposed to isothermal on the 18th of August.

Seeking further evidence, a 24-hour watch was established during which the currents at four depths were measured every 10–15 minutes. At 2330 CST on 21 August 1954 the wind dropped from 3–5 m/sec to calm, followed by a shift of 90–120 degrees and winds of about 1 m/sec after 0030 CST on 22 August. The 1-, 2-, and 10-meter currents slowly decreased to essentially nil by 0100 CST, but the 5-meter current, not far over the thermocline, rose rapidly to about 7 cm/sec by 0125, decreasing again after 0215 (Fig. 1). This increase at depth was associated with a complete reversal of direction (Fig. 2).

Other cases (such as shown in Fig. 3) were observed in which moderate winds and some stratification were the prelude to the appearance of a "jet" at the depth of the thermocline. On no occasion was an increase in wind velocity observed to produce a current variation which might be regarded as similar to or the reverse of that described in the preceding paragraphs.

Examination of the data in Figure 3 reveals the existance of an oscillation superimposed on the increasing current at 6 m after 1930 CST. This oscillation, which is not apparent in the currents near the surface of the lake, has a period of about 25 min and must represent the surface seiche period which is known to be 25.3 min.

DISCUSSION AND CONCLUSIONS

In summary, the observations described above, and others, show that:

1) The sudden decrease of winds strong enough to destroy the slight stratification of the epilimnion *is not* followed by the appearance of a "jet".
2) The sudden decrease of moderate winds blowing over a somewhat stratified epilimnion *is* followed by the appearance of a "jet".
3) Rapid increases of wind *are not* followed by the appearance of a "jet" or equivalent phenomena.
4) Maximum velocities in the "jet" in Lake Mendota are attained in 1½ to 3 hours after inception.

Facts 1) and 2) indicate that the stratification of the epilimnion is important. Since the "jet" represents the appearance of a concentration of kinetic energy at a time when the most obvious source of energy, the wind, has decreased, we must conclude that a source of accumulated potential energy must be available.

The solenoid field produced by the preceding wind in causing the downwind depression of isotherms provided this potential energy (Bryson and Suomi 1952).

Since no such accumulation of potential energy precedes a wind increase, fact 3) would follow from the reasoning above.

The conversion of the potential energy of the depressed isotherms into kinetic energy of currents requires that this thermocline and isotherm tilt decrease. However, this straightening out of the isotherms is nothing more than the internal seiche or temperature seiche of Wedderburn and Williams (1911) and others. It is known (Bryson and Ragotzkie 1954) that the period of the entire internal seiche is 9–11 hours. Thus, the rise to peak velocities should take one quarter of this period or about 2½ hours. On the other hand, the eighth pendulum-day at the latitude of Lake Mendota is about 4¼ hours. Fact 4) thus shows that the "stress-drop jet" in Lake Mendota represents the first swing of the internal seiche rather than an inertial oscillation.

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Artificial Eutrophication of Lake Washington[1]

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ABSTRACT

Lake Washington has been receiving increasing amounts of treated sewage, and appears to be responding by changes in kind and quantity of biota. In 1933 and 1950 the dominant phytoplankton organisms were *Anabaena* and various diatoms and dinoflagellates, but in 1955, apparently for the first time, there was a large population of the blue-green alga, *Oscillatoria rubescens*, a species which makes nuisance blooms in a number of lakes. A great increase in the hypolimnetic oxygen deficit is taken as evidence of increased productivity; the deficit was 1.18 mg/cm²/month in 1933, 2.00 in 1950, and 3.13 in 1955. There is a fairly close relation between the decrease of oxygen and increase in phosphate concentration in the hypolimnion between measurements, a much less close relation with the chlorophyll concentration in the epilimnion.

Many lakes have been made productive by enrichment with domestic sewage or other drainage rich in nutrients. Such enrichment can, over a period of years, greatly modify the character of a lake, converting an oligotrophic lake to a condition of eutrophy, and resulting in the annual production of large populations of algae, usually dominated by the Myxophyceae (blue-green algae). Such populations or "blooms" are notorious nuisances, but these situations are of great interest to limnologists for the insight they permit into the productive processes of lakes. Several such cases were reviewed by Hasler (1947). One of the best studied examples is Zürichsee, Switzerland, which changed in a relatively short time from an oligotrophic lake, with trout, to a eutrophic lake which produces blooms of *Oscillatoria rubescens* and no longer supports trout. Late in the 19th century the summer phytoplankton populations rather abruptly assumed bloom proportions, and about a decade later the cladoceran *Bosmina longirostris* replaced *B. coregoni*. Interestingly, fossil evidence shows that Linsley Pond had the same change of *Bosmina* species during its development at the time it was becoming eutrophic (Deevey 1942).

O. rubescens appears to be an important nuisance in the polluted lakes of Switzerland, and it has been reported in large populations in many lakes in the United States. It was of considerable interest, therefore, to observe that *O. rubescens* occurred in great quantity in Lake Washington during the spring and summer of 1955, probably for the first time. Lake Washington has been receiving treated sewage at an accelerating rate (Fig. 1A). According to figures on the relation of human population to the phosphorus content of sewage-treatment-plant effluent given in Sawyer's detailed paper (1947), and the population associated with the Lake Washington effluent recorded in Fig. 1A, the annual increment of phosphorus to the lake from this source in 1955 would be 37,000 kg, enough to give an average concentration of 0.0132 mg/l (0.426 μg at/l). Nitrogen

[1] Some of the data discussed were obtained with the aid of the State of Washington Research Fund in Biology and Medicine (Initiative 171). We are indebted to Dr. Richard Fleming of the Department of Oceanography for permission to use unpublished data, and data in technical reports obtained by the Department of Oceanography with support by contract N8onr-520/III with the Office of Naval Research. We acknowledge with thanks the help of Dr. Francis Drouet in identifying algae and providing information about distribution, and of Mr. Rufus Kiser in giving information about the occurrence of *Bosmina* in Lake Washington.

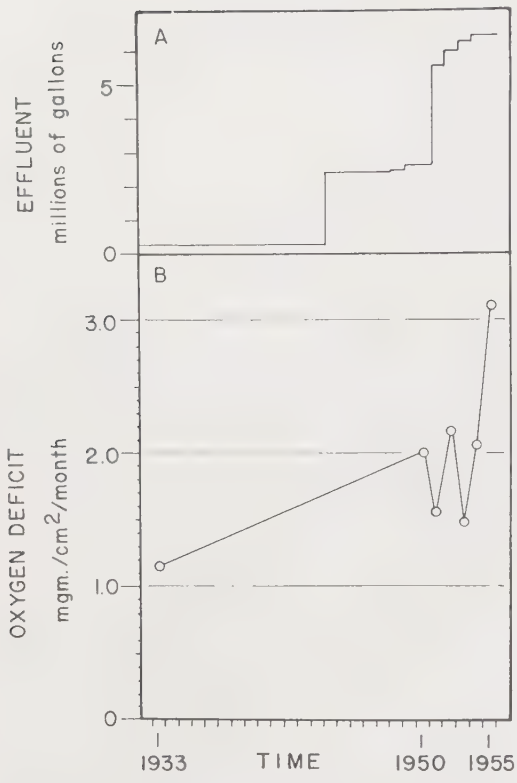

FIG. 1. *A*. Daily capacity of the sewage treatment plants emptying effluent into Lake Washington, 1932–1955. Not included is the amount of untreated sewage and drainage from septic tanks. *B*. Oxygen deficit below 20 meters for the period 20 June–20 August each year, with the exceptions noted in text. The deficit is given on the basis of a 30-day month.

would be 5 times this on a weight basis. Although a detailed budget of sources of nutrients has not been made, it seems very likely that the observed changes in the lake can be attributed to the increased sewage. It seems possible that if enrichment continues the lake may develop serious blooms of the sort experienced in so many other lakes that have similarly been enriched by urban development.

The purpose of the present paper is to describe some of the changes that have taken place since 1933, as far as they are now known. The lake has been studied a number of times. Although the lake was sampled on 9 August, 1913 (Kemmerer, Bovard and Boorman 1923), the earliest detailed work was done by Scheffer and Robinson (1939), Scheffer (1936), and Robinson (1938), including semi-quantitative estimates of plankton populations and analyses of oxygen, phosphorus and nitrogen. Comita (1953) and Anderson (1954) obtained quantitative data on copepods, phytoplankton (including chlorophyll), and some chemical features. The Pollution Control Commission of the State of Washington has presented data on pollution during 1952, and the results of a widespread sampling of surface chemical conditions throughout the year 1952–1953 (Peterson *et al* 1952, Peterson 1955). The University of Washington Department of Oceanography, in connection with a study of salt water intrusion into the lake, obtained data on oxygen, salinity and temperature during the years 1950–1955 (Seckel and Rattray 1953, Collias and Seckel 1954, Rattray, Seckel and Barnes 1954, and unpublished). During the current summer the present authors took data on oxygen, phosphate, temperature and phytoplankton. The most detailed biological information exists for 1933, 1950 and 1955.

The summer standing crop of phytoplankton has increased significantly (Table 1). Except for a strong pulse of *Peridinium* in late August 1950, the 1950 values are consistently much smaller than for cor-

TABLE 1. *Phytoplankton population volume in Lake Washington, calculated on the basis of cell number and cell volume*

Multiply the values shown by 10^3 to get μ^3/ml. Weighted means are given for the period July–August. Epilimnion only.

Date	Total Phyto-plankton	*Oscillatoria rubescens*	*Oscilla-toria agardhi*	*Phormi-dium* sp.	*Aphanizo-menon flos-aquae*
1950					
13 May	2,140	0	84	2	0
24 June	794	0	16	8	0
21 July	211	0	30	4	0
4 Aug	219	0	5	2	0
21 Aug	3,069	0	3	0	0
1 Sept	567	0	9	13	0
15 Sept	762	0	1	105	0
Mean	935				
1955					
1 July	2,895	2,783	0	1	1
14 July	1,407	893	0	8	0
18 Aug	1,755	397	0	610	493
22 Sept	1,314	255	0	125	727
Mean	1,725				

responding times in the summer of 1955. On the basis of chlorophyll content and Secchi disc transparency, it may be stated that the phytoplankton population was somewhat denser on 14 June 1955 than on 1 July, but material is not available for an actual census.

The difference in plankton is indicated further by the fact that the mean summer Secchi disc transparency in 1950 was 3.5 meters (range 3.2–4.0) and only 2.3 (range 1.7–2.8) in 1955. In 1955 the water looked murky and had a striking, somewhat rusty color, due to the pigment in *Oscillatoria rubescens* that gives the species its name.

Qualitatively the plankton was rather different from one period of investigation to another. In 1933 the major components of the summer plankton included *Anabaena lemmermanni* and a number of diatoms. *Oscillatoria* sp. and *Phormidium* sp. were rare at all times. In 1950 the largest populations were due to diatoms in the spring, and dinoflagellates in the late summer. Species of *Anabaena*, other than *lemmermanni*, occurred but did not become abundant. *Phormidium* sp. had a pulse in mid-September, and *Oscillatoria agardhi* formed a relatively large population in February, but *O. rubescens* did not occur. In 1950 the greatest relative abundance of blue-green algae occurred on 15 September when 52% of the plankton volume was composed of *Aphanocapsa* and *Phormidium* cells. The greatest absolute quantity of blue-green algae that year occurred on 11 February when there were 311×10^3 μ^3/l, averaged for the whole lake, of *Oscillatoria agardhi*, amounting to 34% of the total crop. The situation in 1955 was qualitatively very different, for of the maximum counted crop, on 1 July, 96% was composed of *Oscillatoria rubescens*. In 1933 the lake contained *Bosmina longispina* Leydig (= *B. coregoni longispina*), the earlier form in the succession observed in Zürichsee and Linsley Pond. *B. longirostris* was observed in the lake as early as 1940. Thus, the change of *Bosmina* occurred before the appearance of *Oscillatoria rubescens* in Lake Washington, reversing the sequence in Zürichsee.

An interesting ecological problem exists in connection with the two morphologically similar species of *Oscillatoria* that have occurred in Lake Washington, *O. agardhi*, and *O. rubescens*. The replacement of one species by another may imply a distinct, but perhaps subtle, difference in ecological requirements. *O. agardhi* has been observed to form very dense populations in a thin layer in the upper part of the hypolimnion of Hall Lake, Washington, during the summer, and to appear at the surface in moderate quantities only during the early fall (Anderson 1954). In Lake Washington it was abundant only during isothermal conditions, and was about twice as abundant near the bottom of the lake as at the top on the date of the maximum observed populations. *O. rubescens* has frequently been reported in abundance during the winter, although it may occur in great quantity during the summer in the hypolimnion of some lakes (e.g., Findenegg 1943, Thomas and Märki 1949). Nevertheless, it was abundant in the surface waters of Lake Washington during the summer at temperatures up to 20°C, although the large population on 14 June occurred at a temperature of 15°. It has been shown that in Zürichsee, *O. rubescens* adjusts its level to that at which a low light intensity exists (Thomas 1950). Apparently in some lakes this depth is in the epilimnion, in others below it. In the former case, the population is kept distributed through the epilimnion by mixing.

In the absence of direct determinations of photosynthetic rate and of hypolimnetic carbon dioxide accumulation, we have used the oxygen deficit as a measure of productivity (Hutchinson 1938, Ohle 1952). Originally, the deficit was considered simply as the quantity of oxygen necessary to resaturate the hypolimnion at the end of summer stratification. Obviously, the magnitude of the deficit will be related to the size of the hypolimnion and the duration of stratification. The deficits have, therefore, been expressed on an areal basis and as rates in order to make them comparable, following Hutchinson's example. The total amount of oxygen in the hypolimnion was

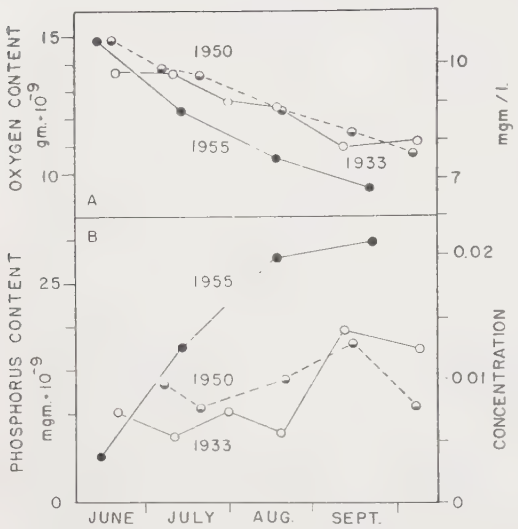

FIG. 2. Total content and mean concentration of oxygen and phosphate phosphorus in the hypolimnion of Lake Washington during three summers. The two scales are related by the fact that the hypolimnion contains 1.407×10^{12} liters. The area of the hypolimnion (20 m) is 61.58×10^{10} cm^2.

calculated for two dates, two months apart, and the later amount subtracted from the earlier. This difference was divided by the area of the hypolimnion and the time difference to give the deficit as mg/cm^2/day. To calculate the quantity of oxygen in the hypolimnion a planimetric method was used. The concentration (mg/m^3) at each depth was multiplied by the area at each depth (m^2), giving a quantity with the units mg/m. These values were then plotted against depth, a line fitted to the points, and the area within the curve measured with a planimeter. The area gives the quantity of oxygen in grams.

The oxygen deficit, calculated for the whole summer, has been found to be, in a series of lakes, roughly proportional to the mean quantity of seston (Hutchinson 1938), and to the mean standing crop of net plankton in the epilimnion (Rawson 1942). While the deficit has previously been used for comparing different lakes, it will be used here for comparing different conditions of the same lake. Anderson (1954), using the oxygen data collected in 1933 by Robinson, and in 1950 by Comita, showed that the oxygen deficit below 15 meters was distinctly higher in the latter year, and that the quantity of phosphate in the hypolimnion was higher also.

For the purposes of the present paper, oxygen deficits have been calculated for all years for which data are available, using a depth of 20 meters to delimit the hypolimnion, in order to avoid any possible effect of sun and of the thermocline, which may extend as deep as 18 meters. The quantity of oxygen in the hypolimnion decreased markedly each summer, but much more rapidly in 1955 than in any of the other years (Fig. 2A). The lowest concentration of oxygen ever measured was 3.50 mg/l at 60 m on 22 September 1955, the most recent date of sampling.

The rate of decrease, or oxygen deficit, was calculated for the period 20 June–20 August, values on those dates being obtained by linear graphical interpolation. The two exceptions are 1952, calculated from 18 July, and 1954, calculated between 9 August and 13 October, there being no suitable earlier determination. The period of calculation was ended on 20 August because after that date in 1950, 1951 and 1952, significant quantities of salt water entered the bottom of the hypolimnion through the ship canal. It would be difficult to make accurate allowance for the amount of oxygen carried in with the salt. The calculations show that while there were irregularities in the oxygen deficit, there has been a definite trend toward increase, and the value for 1955 is much higher than for any previous year studied (Fig. 1B).

The quantity of dissolved phosphate tended to increase in the hypolimnion of Lake Washington during each summer, especially in 1955 (Fig. 2B). The mean summer concentration has increased progressively from 1933 through 1955. The maximum concentration ever observed in the hypolimnion was 0.038 mg/l of P (1.24 μg at/l), also at 60 meters, on 22 September 1955. This value is in contrast to the previous maxima of 0.022 in 1933 and 0.020 in 1950.

Some comments on the mechanism of the relationships between oxygen deficit and epilimnetic processes may be appropriate. The hypolimnetic oxygen is consumed by organisms free in the water, and on and in

the bottom. In a lake of the morphology of Washington, it may be expected that a large proportion of the oxygen consumption takes place in the water, and that the relationship observed depends upon some proportionality between the standing crop in the epilimnion and the amount of decomposable material that settles into the hypolimnion. In some lakes, allowance must be made for photosynthesis in the hypolimnion, but this is inconsequential in Lake Washington because of the low transparency.

The nature of the material in the epilimnion and the processes leading to deposition of part of it into the hypolimnion require further consideration. The material consists of phytoplankton and zooplankton, healthy, moribund, and dead, as well as feces and other organic debris. Obviously, most of the dead material, tripton, is capable of settling into the hypolimnion where it can support bacteria and other organisms which consume oxygen. But even some living phytoplankters can be expected to settle out and consume oxygen, at first through their own respiration, and later as substrate for bacteria. Many of the zooplankton which spend the day in the deep water presumably migrate to the epilimnion and feed there at night. Thus, some of the respiration of healthy hypolimnetic planktonic animals represents use of material produced in the epilimnion. A very important process, leading to sedimentation of particulate materials into the hypolimnion, is the grazing activity of the zooplankton, through which organisms are removed from the water, and the partly digested remnants dropped as feces. It has been shown in a marine population that there is a fairly close proportionality between the density of the phytoplankton population and the abundance of copepod feces in the water, suggesting that the animals tended to cram materials through the gut as fast as they could collect it (Harvey, Cooper, Lebour and Russell 1935). There is no reason to suppose that similar freshwater copepods behave differently.

Therefore, under ordinary circumstances, the animals can be expected to collect more food and drop more feces per unit time when phytoplankton is abundant than during periods of scarcity. The larger the crop of zooplankton, the greater the total feeding rate will be. Also, large plankton crops will produce corpses faster by reason of senescence and parasitism than will small ones. Therefore, lakes which develop relatively large populations of organisms of almost any kind in the epilimnion might be expected to have relatively large hypolimnetic deficits.

The low correlation actually observed by Hutchinson and Rawson between standing crop and oxygen deficit is due in part to the biological and chemical diversity of material going into the hypolimnion. The real relationship, however, must be with the primary productivity of the epilimnetic population, and this must, in the end, be more important than the population size or composition itself. If the phytoplankton population is reproducing slowly, relative to its rate of removal, then the standing crop will decline, and the average size will be small. On the other hand, a rapidly reproducing phytoplankton population could be kept grazed down by an active zooplankton population for much of the summer (see, for example, Anderson, Comita and Engstrom-Heg 1955). Naturally, a long-continued high phytoplankton production can ordinarily be expected to give rise in time either to a large phytoplankton population or to a large zooplankton population, but the fact that increased phytoplankton may result in increased transport to the hypolimnion, out of proportion to the assimilation by the zooplankton, means that the oxygen deficit will probably be more closely related to productivity than to standing crop. The looseness of the relationship obtained by Rawson and by Hutchinson may measure the low degree to which mean standing crop is an indication of productivity in the particular lakes involved.

One might also expect to find relationships between epilimnetic and hypolimnetic events during different short periods in one summer, although the nature of the relationships would be affected by the rate at which the various materials settle out, and the rate at which they are decomposed (Kleerekoper 1953). Accordingly, short term deficits were calculated for the period be-

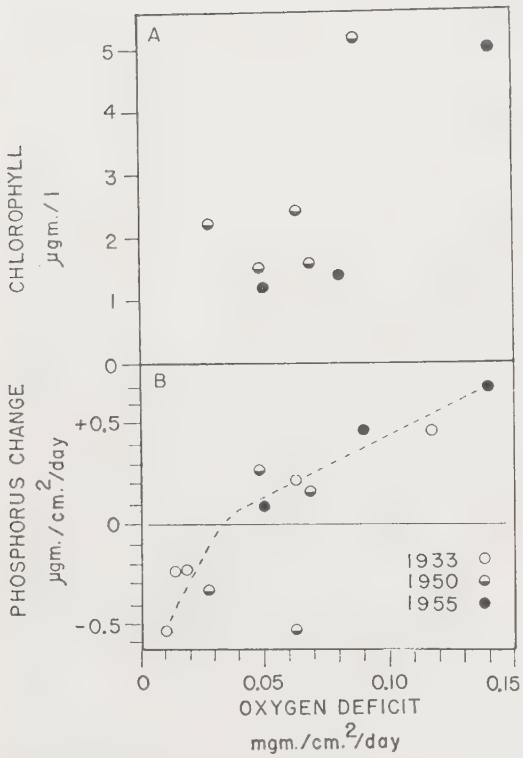

FIG. 3. Relation of oxygen deficit, calculated for short periods, to chlorophyll concentration in the epilimnion at the beginning of the period, and to the rate of change of phosphate phosphorus in the hypolimnion during the same periods.

tween measurements of oxygen in the years in which the most data were taken. This is not the place for a discussion of the ecological significance of chlorophyll in plankton populations beyond pointing out that a case can be made for the use of chlorophyll as a measure of potential primary productivity (Manning and Juday 1941, Edmondson 1955), and that it is reasonable to expect a positive relation between epilimnetic chlorophyll and the oxygen deficit. There was indeed a tendency for the largest decreases in hypolimnetic oxygen to take place during periods when the initial concentration of chlorophyll was large, but the relation is not strong (Fig. 3A). The fact that the correlation is this low calls for further investigation.

Although heterotrophic bacteria are capable of absorbing phosphate, as well as causing it to be released from phosphorus-containing substrates, phosphate liberation in the hypolimnion is related in some degree to the processes that lead to removal of oxygen. In order to establish the relationship, the rate of change of phosphate content of the hypolimnion was calculated in the same way as the oxygen deficit (Fig. 3B). There is a distinct tendency for the larger rates of increase of phosphate to occur with high oxygen deficits, and with but one exception, decreases in phosphate are accompanied by slow decreases of oxygen. The exceptional point is for the period 15 September–7 October 1950, at a time when there had been a relatively large intrusion of salt water into the hypolimnion, but the large oxygen deficit cannot be attributed solely to the oxygen content of this water. The slope of the upper part of the curve, associated with increases in phosphate, shows that in the hypolimnion of Lake Washington 1 atom of phosphorus is liberated as phosphate for every 16.4 atoms of oxygen removed. This is a very much lower O/P ratio then has been observed in the regeneration of phosphorus in the open sea (Redfield 1942), and in the converse release of oxygen by phytoplankton in photosynthesis (Edmondson and Edmondson 1947, Edmondson 1955). It seems to indicate an effective regeneration of phosphate, relative to carbon, even allowing for probable amounts of anaerobic activity in the bottom, and may be a result of the nutritive conditions permitting the algae to develop unusually high phosphorus contents. It would be very interesting to know what the relation is in a large series of lakes with very different deficits and nutrient supplies.

In summary, Lake Washington shows definite evidence of having rather suddenly increased in productivity, the oxygen deficit in 1955 being 1.8 times that in 1952, the previous maximum, and 2.7 times the rate in 1933. The biological character of the lake has recently changed in that the former dominance of diatoms and dinoflagellates in the population has been replaced by that of the blue-green alga, *Oscillatoria rubescens*, a species that forms nuisance blooms in a number of European and American lakes. The most reasonable explanation of the

increase in productivity is the great increase in treated sewage added to the lake with the growth of adjoining communities. Lake Washington seems to be fitting the pattern of abrupt change, as seen in the other cases of polluted lakes which have been studied limnologically before pollution became serious. It is hoped that it will be possible to study Lake Washington further as its eutrophication proceeds or, if the effluents are diverted, to see to what extent the lake regains its former more oligotrophic condition.

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Observations on Dinoflagellate Blooms[1]

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ABSTRACT

Dinoflagellate blooms were observed in Delaware Bay from 1952 to 1954 and in tidal creeks on Sapelo Island, Georgia, during 1955. In all cases the blooms were concentrated at the surface of the water. The organisms were positively phototactic and swam toward the light at 0.3 to 0.8 cm/sec. Because of their tendency to remain at the surface, the dinoflagellates were concentrated by weak convergences.

One of the blooms was associated with unusual rainfall but the others occurred during dry weather. The concentrations of phosphorus found in the blooms could be accounted for on the basis of concentration mechanisms without postulating a special nutrient source, such as river flow. However, river flow may contribute other biologically important substances.

INTRODUCTION

Two general mechanisms have been proposed for the origin of dinoflagellate blooms. One involves a special nutrient source, which will make possible a rapid multiplication of dinoflagellates within the region of abundant nutrients. The other involves the concentration of dinoflagellates at a time when they are abundant or dominant in the phytoplankton. A number of special nutrient sources have been suggested. Among the most commonly accepted are upwelling of water from below the euphotic zone (Brongersma-Sanders 1945, 1948; Gunther 1936) and runoff from the land, particularly a pulse of river flow after heavy rains (Slobodkin 1953, Conover 1954). Several concentrating mechanisms have been proposed, and all of them depend on a positive phototaxis of the dinoflagellates. Thus, in the light some species of dinoflagellates will congregate at the surface of the water or at a depth of optimum light intensity (Hasle 1950, 1954; Ryther 1955, Slobodkin 1953). Having swarmed at the surface, they may be further concentrated by several mechanisms. Chew (1955) has found evidence for a large-scale convergence in the "red tide" area off the West Coast of Florida. Ryther (1955) has suggested several smaller-scale mechanisms: concentration against a shore by onshore winds, concentration between pairs of wind-induced current vortices, and concentration at convergences where water masses of different density are mixing.

Ryther (*Ibid.*) points out that the presence of a concentrating mechanism makes it possible to explain the high nutrient concentrations found in dinoflagellate blooms without postulating a special nutrient source. However, the two are not mutually exclusive, and conceivably both might act together in some cases to bring about a bloom.

This paper presents observations on dinoflagellate blooms in Delaware Bay and in tidal creeks on Sapelo Island, Georgia. Dinoflagellate blooms have not been described previously in Georgia estuarine waters, but they have been described in Delaware Bay. Martin and Nelson (1929) found that the Delaware Bay blooms were usually elongated patches or belts as much as a mile in length, and that the waves passing through the belts were smoothed "as though in an oil slick". The principal bloom organisms were *Amphidinium fusiforme* Martin and *Gymnodinium splendens* Lebour. Martin and Nelson attributed the unusual concentration of organisms to the cohesion of the gelatinous envelopes of the

[1] Joint contribution of the Oyster Research Laboratory, New Jersey Agricultural Expt. Sta., and the Marine Biology Laboratory, University of Georgia.

dinoflagellates. The significance of slicks was not then recognized. Langmuir (1938) explained the physical basis of most slicks, and their biological significance was shown by Woodcock (1944, 1950), Dietz and Lafond (1950), and Ewing (1950).

Woodcock showed how buoyant objects or organisms are caught and concentrated in wind-induced convergences. Ragotzkie and Bryson (1953) found that *Daphnia pulex* is similarly concentrated in convergences, since it actively attempts to remain at a constant depth.

The valuable assistance of Mr. Frank B. Flower and Mr. William A. Richards of the N. J. Oyster Research Laboratory in the collection and analysis of the Delaware Bay samples is gratefully acknowledged. Miss Mary L. Robbins also aided in the analysis of samples and tabulation of data.

MATERIALS AND METHODS

The phosphorus content of the water and suspended particulate matter, including plankton, was estimated by the method of Redfield *et al* (1938), using a Fisher electrophotometer to read the density of color developed. The phosphorus fractions were separated and the inorganic fraction estimated within four hours of collection. The values given for total phosphorus in the Georgia blooms were estimated by the method of Hansen and Robinson (1953).

Total chlorophyll was estimated by filtering water samples through a layer of barium sulfate precipitated on Whatman No. 42 filter paper. The pigments were extracted in 80 per cent acetone and the optical density of the extract measured in the Fisher electrophotometer, using a red filter with transmission maximum at about 660 mμ. The standard curve used for estimating chlorophyll concentration was prepared with 80 per cent acetone solutions of pure chlorophyll *a*.

Salinity was measured by the Knudsen silver nitrate titration.

Surface temperature was measured with bucket-type thermometers. Subsurface temperature was measured with reversing thermometers. Appropriate corrections of the raw readings of each type of thermometer were applied when necessary.

Wind velocity was estimated from observations of the state of the sea in open water and recorded in Beaufort scale units.

Daily river discharge data for the Delaware River and other rivers entering Delaware Bay and the lower Delaware River were provided by the U. S. Geological Survey. We acknowledge with thanks their release of unpublished data.

Cell counts were at first made in a haemacytometer. However, the following method proved superior. A carefully shaken aliquot (1–100 ml) of raw sea water was passed through a millipore filter. The volume of aliquot was determined by trial to give a sufficient density of organisms on the filter to permit a count of about 1000 cells in a reasonable number of fields. The fresh, thoroughly wet filter was placed on a microscope slide, and the organisms were counted, using substage illumination. The dinoflagellates were flattened against the filter but they could be identified readily.

In several comparative trials mean haemacytometer counts were higher than millipore filter counts by a factor of 2 to 4. Replicate haemacytometer counts did not have a normal frequency distribution, and the individual counts were either zero or a large number. Replicate millipore counts were normally distributed about the mean with quite satisfactory confidence limits. This suggests that in this case at least clumping and settling errors were involved in haemacytometer counts of dinoflagellates.

OBSERVATIONS

Delaware Bay

Blooms were found in virtually all parts of Delaware Bay below Ben Davis Point. Some were just visible as a reddish or brownish color. Others were so dense that the water appeared to be filled with clumps of flocculated material and was abnormally viscous. The blooms occurred in spring, summer, or fall, but only when the surface water temperature was between 25 and 29°C. The organisms were identified by Dr. Robert Renlund. In every case they were a mixture of *Amphidinium fusiforme* and *Gymnodinium splendens*.

TABLE 1. *Observations on dinoflagellate blooms in Delaware Bay from 1952 to 1954*

Date	Location	Depth, meters	Temp., °C	Salinity ‰	Phosphorus, microgram atoms per liter				Total chlorophyll micrograms/liter	Remarks
					Inorganic phosphate	Dissolved organic	Particulate	Total		
9–13–52	Miah Maull, 39°06.8′ N, 75°12.8′ W	0.1	27.0	16.6	4.0	4.3	4.2	12.5	280	In bloom
		3		26.8	1.3	0.7	0.5	2.5	20	
		0.1	26.0	17.4	1.2	1.1	0.9	3.2	30	Outside bloom
		3		27.0	1.1	0.8	0.2	2.1	4	
6–22–53	Benny's 39°15.6′ N, 75°17.7′ W	0.1	24.5	12.3	0.4	0.9	2.9	4.2	160	
		0.1	25.3	11.9	0.1	0.3	1.4	1.8	60	
6–23–55	Hog Shoal, 39°15.4′ N, 75°15.3′ W	0.1	26.1	12.4			16.9	21.2	360	
		3	24.0	12.9			1.2	1.8	40	Dense bloom
		6	23.8	12.9			0.7	0.9	30	
6–12–54	Maurice River Cove, 39°11.0′ N, 75°02.4′ W	0.1							100	
6–13–54	Maurice River Cove, 39°10.5′ N, 75°03.6′ W	0.1	25.3	17.0					50	
		0.1							80	Streaks
		2	23.8						20	hardly visible

The bloom observed in the fall of 1952 (Table 1) was in a surface layer of relatively fresh water. The salinity gradient was one of the sharpest we have observed in Delaware Bay. The weather conditions preceding the bloom are striking: after six weeks without rain there were two days of general rain over the Delaware watershed, producing a pulse of river flow which was observed nine days before the bloom was discovered. The other blooms observed in Delaware Bay occurred during periods of exceptionally dry weather and uniformly low river flow. All the Delaware Bay blooms occurred during periods of light winds, not exceeding Beaufort force 2. On one occasion a patch disappeared when the wind rose from force 2 to 3. The blooms were all limited to the surface layer of the water, even in the absence of a significant density gradient. In addition to being concentrated at the surface, the blooms were typically in the form of elongated slicks with abrupt margins. This was also true in the 1952 bloom. The count of organisms (by haemacytometer) in the surface water of the bloom of June 23, 1953 was 38×10^7 per liter, over 99 per cent of which were dinoflagellates.

No mortality of marine organisms was associated with the blooms. However, a few days after the appearance of the 1952 bloom local oyster packing companies began to complain of "red oysters". The red material was concentrated in the digestive glands of the oysters. After several days in cold storage the liquor of the shucked oysters became blood-red. Several weeks later, oysters in nearly all parts of Delaware Bay had developed dark red digestive glands. They no longer exuded red liquor after being shucked, and the wet volume of meats per bushel of oysters increased from 4 or 5 pints per bushel to 8. These values are based on the weekly production record of one shucking house. The blooms of 1953 and 1954 did not occur during oyster packing season, so that their immediate effect on oysters is not known. Some oysters examined in the fall of 1953 had faintly pink digestive glands but did not exude red juices. Red oysters associated with abundant dinoflagellates have been reported by Nelson (1948).

On several occasions when samples from blooms were brought into the laboratory it was noted that they showed marked positive

phototaxis. When placed in a glass container, they assembled on the side of the container nearest the light.

Sapelo Island, Georgia

One of the blooms observed at Sapelo Island occurred in the headwaters of the Duplin River, a small tidal river with essentially no fresh-water input and no vertical or horizontal salinity gradient. The hydrography of the Duplin River has been described by Ragotzkie and Bryson (1955). The bloom occurred during unusually warm weather for the season, after a period of gradual warming. The mean maximum air temperature for the period immediately preceding the appearance of the bloom (Feb. 20–28) was 20°C. The mean maximum air temperature while the bloom was expanding rapidly (Mar. 1–4) was 26.5°C. The water temperature in the bloom reached 20° shortly after the bloom reached its maximum development. There was no rain from Feb. 11 until after the bloom had disappeared.

Transparency of the water in the upper Duplin River, measured with a Whitney densitometer with self-contained light source, was unusually high before the bloom. The high slack water reading on Feb. 17 was 89 per cent transmission and on Feb. 18 it was 80 per cent. Typical values for this location are 40 to 65 per cent. The unusually high values coincided with a period of neap tides.

Counts were made of composite surface water samples on several successive days, using the millipore filter method. The bloom was first seen on Feb. 28, 1955, and at that time it was limited to small patches along the banks of the upper end of the river. The bloom reached its maximum development on March 5. At that time the count at the surface in the center of the bloom was 19 ± 5.1 (standard deviation) $\times 10^6$ cells per liter, diminishing to $2.7 \pm 1.0 \times 10^4$ cells per liter at a point 2 kilometers downstream. The last counts, made on March 10, had a maximum of $3.3 \pm 0.6 \times 10^5$ cells per liter, diminishing rapidly downstream. More than 99.9 per cent of the phytoplankton in the bloom area was *Gymnodinium* sp., except at the downriver end of the bloom where there was some intermixture with *Peridinium* sp.

TABLE 2. *Surface observations on dinoflagellate blooms, Sapelo Island, Georgia, 1955*

Date	Location	Salinity, ‰	Temp., °C.	Total phosphorus, microgram atoms/liter
3–3–55	Duplin R., 31°29.4′ N, 81°16.0′ W	12.3	19.4	6.0
3–3–55	Duplin R., 107 m. downstream	12.6	19.5	4.5
3–3–55	Duplin R., 375 m. downstream	12.6		3.5
3–3–55	Duplin R., 758 m. downstream	12.4		3.2
4–21–55	Boat basin, Sapelo Island		22.8	25

Transparency measurements with the Whitney densitometer showed a considerable concentration of the organisms in the upper 10 centimeters of the water column. There was some tendency for concentration of the organisms against the downwind shore of the river, particularly during the slack water periods. However, total phosphorus in the bloom (Table 2) was not appreciably greater than at other times in the same location.

Another bloom appeared in a shallow boat basin at the south end of Sapelo Island on April 21, 1955. The same species of *Gymnodinium* apparently was involved. During the day the bloom was largely concentrated in the uppermost 10 centimeters of the water. At night and in the early morning it was not to be found, but it re-formed each day for 4 days at about 0900. The bloom was concentrated in several patches near the downwind shore of the basin. To demonstrate the presence of regions of surface convergence, free current drags 10 centimeters in depth and ballasted to float in the upper 10 centimeters of water were released, widely spaced, across the center of the basin. They drifted to a point near the downwind shore, where they remained, close together, in the center of a dense concentration of dinoflagellates.

When samples from the bloom were taken into the laboratory it was found that if the organisms were kept in total darkness they remained randomly dis-

tributed in the water. After 10 hours a few began to attach to the sides of the container and surface film of the water, but most of the dinoflagellates remained swimming at random for 48 hours. However, if after the first hour in darkness the container was placed in the light, the dinoflagellates quickly assembled on the side of the container nearest the light source. By covering part of the vessel and periodically changing its orientation to the light it was possible to measure the swimming speed of the dinoflagellates over a path of 10 centimeters. Estimates varied from 0.3 to 0.8 cm/sec.

DISCUSSION AND CONCLUSIONS

All of the dinoflagellate blooms showed a strong tendency to swarm at the surface in daylight. In addition, at least two concentrating mechanisms could be identified. In Delaware Bay, where the blooms were in open water, their presence in the form of slicks and the abruptness of their margins (cf. Martin and Nelson 1929, Fig. 1) suggests that the dinoflagellates are being concentrated in weak convergences. Probably these are the zones of convergence between pairs of wind-induced current vortices (cf. Ryther 1955, Fig. 5).

The observation that blooms occur only during light winds suggests that at wind velocities of Beaufort 3 or more the speed of the current vortices exceeds the swimming speed of the dinoflagellates. The present observations of swimming speed of *Gymnodinium* sp., as well as those of Peters (1929) and Hasle (1950, 1954) suggest that some species of dinoflagellates can oppose successfully a vertical current of about 1 cm/sec. Langmuir's (1938) measurements suggest that this vertical velocity is exceeded in wind-induced vortices somewhere between Beaufort 2 and 3. The Georgia blooms, occurring in sheltered creeks, were concentrated near the downwind shore. Convergence was demonstrated in the densest part of one of the blooms. Because of their sheltered situation, they persisted at higher wind speeds than did the Delaware Bay blooms.

The formation of a dinoflagellate bloom will depend on an adequate supply of essential nutrients, including not only nitrogen and phosphorus but also trace elements, vitamins, and possibly other organic materials (Collier 1953, Provasoli and Pintner 1953, Wilson and Collier 1955). Slobodkin (1953) and Conover (1954) suggest that the origin of these nutrients is in fresh water from rivers. The evidence from the blooms in the present study, as well as those of Ketchum and Keen (1948) and Chew (1953) is that fresh water from rivers does not contain large amounts of phosphorus and is not the source of the high phosphorus values observed. Ketchum and Keen point out that if dinoflagellates swarm at the surface, as they have since been shown to do by Slobodkin (1953), several others summarized by Ryther (1955), and the present writers, they may produce a tenfold concentration of phosphorus in the surface water. If some concentrating mechanism, such as wind-induced vortices, is present, a much greater concentration of phosphorus can be expected. In all the blooms in the present study, the observed phosphorus concentrations can be accounted for in this way, without postulating a special nutrient source. In the 1953 Delaware Bay bloom (Table 1) there is a depletion of phosphorus in the subsurface water. Normal values for total phosphorus in Delaware Bay are 2 to 3 microgram atoms per liter. Subsurface depletion is not evident in the 1952 bloom, because the subsurface sample was taken below the shearing plane between the brackish surface water and the subsurface water. The surface temperature difference between the sample taken in the bloom and that taken outside it strongly suggests convergence in the bloom and divergence outside it, i.e. a current vortex. However, the vortex would extend down only to the halicline.

It is, of course, possible that in the 1952 bloom the surface water contained unusual amounts or kinds of plant nutrients. However, the samples taken were so spaced that they provide no information on this point. The phosphorus concentration of about 4 times the normal could be accounted for on the basis of a pair of current vortices extending down only a meter or two.

If fresh water from the land is a factor in initiating dinoflagellate blooms, the actual causative agent must be either a favorable response to lowered salinity or the presence of essential trace elements or organic substances in the fresh water. Before the influence of trace metals, vitamins, or other organic materials can be determined, improved field methods for their quantitative estimation are needed. This remains one of the most serious deficiencies in our knowledge of the causative factors of dinoflagellate blooms.

The Duplin River bloom of March, 1955, apparently developed without a special nutrient source and without a significant amount of concentration. There was no rainfall before or during the bloom to bring in nutrients, and the only other source of fresh water is through the mouth of the river. Since total phosphorus values in the bloom were normal for that area and season, there was evidently not enough concentration by phototaxis in the shallow water of the river to produce a local increase in phosphorus. However, the water was rich enough in phosphorus to support the bloom.

We may speculate that a partial explanation for the appearance of the bloom may be found in the weather conditions preceding and during the bloom. A period of rapid warming was combined with unusual water transparency in a usually turbid tidal river. This may have produced an environment unusually favorable to dinoflagellate production.

Dinoflagellate blooms in general give the appearance of a burst in production. In the Duplin River bloom discussed above photosynthesis was proceeding at an exceptionally rapid rate. The marked increase in oyster meat yields following the 1952 Delaware Bay bloom suggests that there was a general increase in production in this case also. In the other blooms observed there is no evidence of an increase in production, but actual production measurements are lacking.

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Photosynthesis in the Ocean as a Function of Light Intensity[1]

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ABSTRACT

Photosynthesis was measured in 14 species of marine plankton algae in relation to light intensites within the entire range to which natural phytoplankton populations may be exposed. A mean curve was constructed showing relative photosynthesis in marine phytoplankton as related to light intensity. From this curve and surface radiation data, relative values for photosynthesis were determined throughout the day at the surface and at depths in the ocean at which the surface intensity is reduced by given amounts. Integration of these values over the entire day gave values for daily relative photosynthesis at each depth considered, and integration of the daily values with depth resulted in a single figure for daily relative photosynthesis beneath a unit of sea surface.

An empirically derived relationship was discovered between daily surface radiation and daily relative photosynthesis within the water column. From this relationship the effect of light intensity upon photosynthesis throughout the year at a temperate latitude was demonstrated.

A preliminary method is described for estimating absolute daily photosynthesis beneath a square meter of sea surface from measurement of (1) photosynthesis of a sample of the population at light saturation, (2) the extinction coefficient of light in the water, and (3) the daily surface radiation.

From an estimate of the ratio of photosynthesis to respiration at light saturation, the daily ratio $P:R$ for the entire population is calculated. It is shown that phytoplankton populations cannot photosynthesize sufficiently to compensate for their own respiration during periods of low solar radiation, as may occur in the winter months at temperate or northern latitudes.

INTRODUCTION

Although light is the most important limiting factor to photosynthesis in the ocean, the effects of light intensity upon the photosynthetic rate of the principal group of marine plants, the plankton algae, has never been adequately investigated. Laboratory studies appear to be confined to some experiments by Barker (1935) with the diatoms *Nitzschia closterium* and *N. palea* in which both light intensity and photosynthesis are expressed in relative units. In the field, Jenkin (1937) measured simultaneously light intensity and photosynthesis by the diatom *Coscinodiscus excentricus* at various depths in the English Channel, producing what has persisted as the only quantitatively useful information on the subject with respect to marine phytoplankton.

There exists a large literature dealing with the relationship between light intensity and photosynthesis in terrestrial plants, aquatic phanerogams, and a few freshwater algae, notably *Chlorella*. This has been reviewed by Rabinowitch (1951, chap. 28), showing the same general trend in every case of a linear increase of photosynthesis with light intensity up to a saturation point, beyond which higher intensities do not increase photosynthesis but eventually result in an inhibition, the physiology of which is discussed by Steemann Nielsen (1952). The majority of laboratory studies with terrestrial or freshwater plants have not been concerned with the high intensities at which this inhibition occurs, but the phenomenon has been clearly demonstrated in all measurements of photosynthesis in natural waters by a marked depression at or near the surface where the organisms are exposed to nearly full incident solar radiation (Marshall and Orr 1928, Jenkin 1937, Steemann Nielsen 1951, 1952).

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The following report will describe some experiments in which the relationship between photosynthesis and light intensity has been investigated in 14 species of marine plankton algae within the wide range of light intensities to which they may be exposed in nature. On the basis of these experiments an attempt will be made to construct a general photosynthesis-light curve for marine phytoplankton, which in turn will serve as a basis for some speculation on the effect of light upon total photosynthesis and the ratio of photosynthesis to respiration within the euphotic layer of the ocean.

EXPERIMENTAL METHODS

Photosynthesis measurements were made on the roof of the Woods Hole Oceanographic Institution during June and July, 1955, using solar radiation as a light source. Incident light measurements were made with a calibrated Weston Model 594RR photoelectric cell and are reported in foot-candles. Experiments were conducted for four-hour periods consisting of the two hours before and after noon, and were confined to bright sunny days with no appreciable cloud cover. The incident solar intensity increased during the first half and decreased during the latter half of the experiments, but did not vary from the mean intensity within the four-hour period by more than 8%.

Photosynthesis was measured in 20-ml glass-stoppered bottles which were placed in a light-tight box divided into 9 compartments. Each compartment held three bottles so that three experiments could be conducted simultaneously. The compartments were then covered with a graded series of neutral density filters prepared from exposed photographic plates. The absorptive indices of the filters were determined by photometric measurements made within each compartment, which thereby also took into account influences of the container itself upon the radiation.

The bottles were suspended on wire rods above a flat, black surface so that reflected light was negligible. The bottom of the compartments were open to the air but shielded from the light by a system of baffles. The temperature in the entire series of experiments ranged from 18–23°C but did not vary between bottles in any one experiment by more than 1°C.

Photosynthesis was measured by the uptake of $C^{14}O_3^=$ using essentially the same technique described by Steemann Nielsen (1952). However, to permit comparison of the different species, photosynthesis at each intensity (P_l), as determined by the activity of the organisms after exposure, is reported relative to the maximum photosynthesis (P_{max}) observed in the same experiment (P_l/P_{max}).

The cultures used for the experiments were routinely grown at 20°C under 1000 foot-candles of illumination provided by daylight fluorescent lamps. They were approximately one week old when used, at which time they were diluted with enriched Millipore-filtered seawater to such a density that no appreciable absorption of light could be detected through the thickness of the experimental vessel (3.2 cm). In order to eliminate any short-term effects of suddenly exposing the organisms to light intensities different from those at which they had grown, the bottles containing the algal suspensions were placed in their appropriate compartments in the experimental box and exposed to the sun for approximately two hours before the start of the experiment at which time the C^{14} was added with a hypodermic syringe.

In addition to 28 experiments with organisms grown in the manner described above, three additional experiments were made with cultures which were grown on the roof of the building and hence exposed to full sunlight.

Finally a third type of experiment consisted of measuring photosynthesis by the same method as described above and during the same four-hour, mid-day period, at various depths in Woods Hole Harbor. The simultaneous measurements of incident radiation and the extinction coefficient of the water permitted the calculation of the light intensity at each depth at which photosynthesis was measured. These experi-

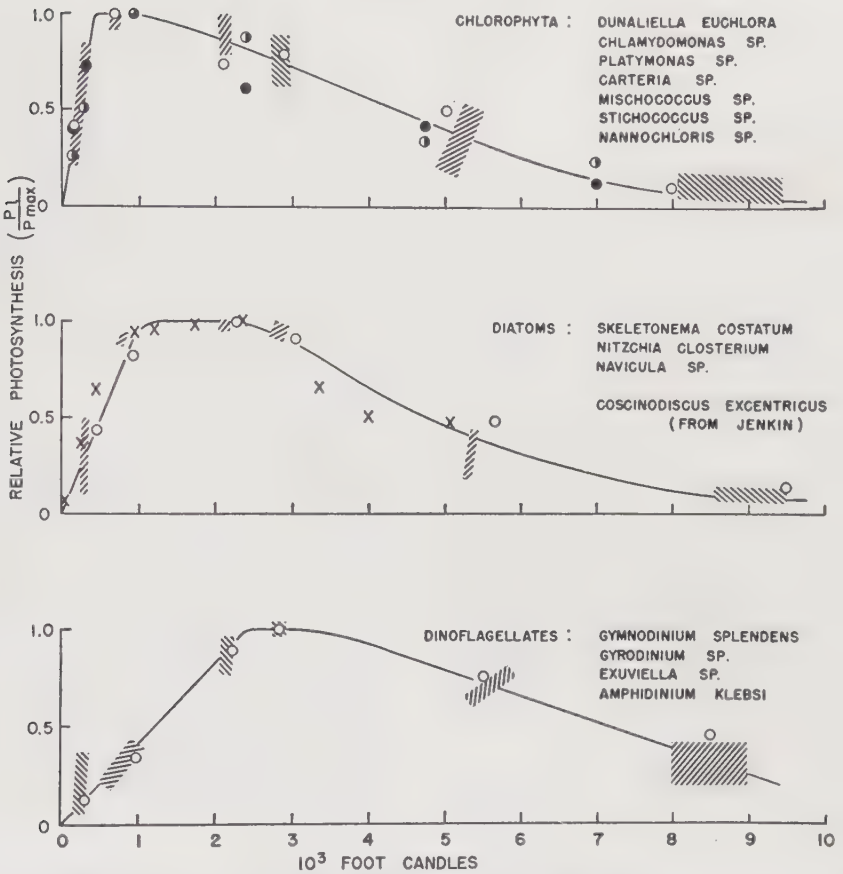

FIG. 1. The relation between photosynthesis and light intensity in some marine phytoplankton. Rectangles represent scatter of points in experiments using cultures grown at 1000 fc and measured with neutral density filters. Open circles are cultures grown under natural sunlight. Filled and half-filled circles are cultures grown at 350 and 1500 fc and measured in Woods Hole Harbor. Crosses from Jenkin (1937).

ments were made with the green flagellate, *Dunaliella euchlora*, which had been grown in the laboratory at light intensities of 350 and 1200 foot-candles.

A total of 14 species of phytoplankton were used in these experiments including seven green algae, three diatoms, and four dinoflagellates. The species are listed in Figure 1. *Gymnodinium splendens* was obtained from Dr. Beatrice Sweeney, *Gyrodinium* sp. and *Exuviella* sp. from Dr. Luigi Provasoli, and *Amphidinium Klebsi* and *Dunaliella euchlora* from Dr. R. R. L. Guillard. The remaining organisms were isolated by the author from marine or brackish water near Woods Hole.

INTERPRETATION OF THE DATA

The uptake of C^{14} measures only photosynthesis above compensation, or photosynthesis minus respiration (Ryther 1954). Thus the point of zero apparent photosynthesis occurs at the compensation intensity, or somewhere between 50 and 100 foot-candles, and the resulting curve shows the relationship between light intensity and net photosynthesis. However, since respiration is constant, the curve for total photosynthesis lies parallel to the net photosynthesis curve and passes through the origin. The curves relating intensity and total photosynthesis which will be described below were

constructed on the basis of this relationship from net photosynthesis measurements.

Although there is evidence that photosynthesis below the compensation intensity proceeds with twice the efficiency as that above that point (Kok 1951), the increase is shown here as being linear from zero light intensity to saturation. However, the error resulting from this assumption is negligible and photosynthesis below 50 foot-candles has been considered as insignificant for the purposes of this report.

RESULTS

There was a remarkable similarity in the behavior of the organisms within each of the three taxonomic groups (green algae, diatoms, and dinoflagellates) and a rather striking difference between those of different groups. For this reason the data for each group are shown separately (Fig. 1). Within each group, the scatter of data in different experiments with the same species was as great as that between different species, so the results for the individual species are not shown.

Saturation intensity was reached for the Chlorophyta at 500–750 foot-candles, for the dinoflagellates at 2500–3000 foot-candles, and at intermediate intensities for the diatoms. Inhibition of photosynthesis became apparent in all three groups within about 1000 foot-candles of saturation. At intensities of 8000–10000 foot-candles, comparable to full noon sunlight, photosynthesis in the Chlorophyta and diatoms was only 5–10% of that at saturation, while photosynthetic activity in the dinoflagellates was reduced somewhat less to 20–30% of maximum.

Cultures of one species of each group—the green flagellate, *Dunaliella euchlora*, the diatom *Skeletonema costatum*, and the dinoflagellate, *Amphidinuim Klebsi*—were grown on the roof of the laboratory where they were exposed to full incident radiation. During their growth period of one week there were one rainy day, two overcast days, and four bright, clear days. The cultures grew slowly and showed marked chlorosis, but both flagellates remained motile and all were later successfully subcultured under normal laboratory conditions.

Photosynthesis-light intensity experiments similar to those discussed above were made with these cultures at the end of seven days. Although their uptake of C^{14} was low, the relative rates at different light intensities were essentially the same as that of the same organisms grown in the laboratory under 1000 foot-candles (see Fig. 1). There was no indication of adaptation to the high intensities to which they had been exposed.

Photosynthesis of the flagellate, *Dunaliella euchlora*, was also measured at depths of 0, 1, 2.5, 5, 7.5 and 10 meters in Woods Hole Harbor. The extinction coefficient was obtained by lowering a submarine photometer (a Weston Model 594RR photoelectric cell) and measuring the reduction of light. The water was homogeneous with respect to light extinction within the upper 10 meters with a coefficient (k) of 0.40. No significant loss of radiation through reflection at the surface could be detected. Incident radiation was measured as before with a recording Weston photoelectric cell.

Cultures were used which had grown for two weeks in the laboratory at light intensities of 350 and 1200 foot-candles. Those which were grown at the lower light intensity contained 4.3 times as much chlorophyll *a* per cell, and their photosynthetic rate per cell was 3–4 times that of the cells grown at light saturation. But the relative response of the two cultures to different light intensities was essentially identical and comparable to that found in the roof experiments with neutral density filters and with cultures grown at 1000 fc (Fig. 1: Chlorophyta).

Figure 1 also shows for comparison some of Jenkin's data for the diatom, *Coscinodiscus excentricus*. The data were taken from her Figure 9 (p. 333) showing oxygen production per hour plotted against average energy per hour. The July 25 measurements were chosen for the comparison since on that day "the sea was calm, the light was very bright, and conditions were relatively constant throughout the exposure".

Light values, which were originally

measured in photometric units and converted to energy units by Jenkin, were reconverted to foot-candles to permit comparison with the present data, using the same conversion factors employed by Jenkin. A reasonably good fit of Jenkin's data to the author's diatom curve is obvious.

Despite the variability of the photosynthetic response to light intensity of the different taxonomic groups, an attempt has been made to construct a general photosynthesis-light intensity curve for marine phytoplankton. This has been done by averaging the relative photosynthesis values at each light intensity for the three groups of algae as given by the curves in Figure 1. Because the Chlorophyta are relatively unimportant in the marine phytoplankton, they have been weighted only one-half as heavily as the other organisms in obtaining the average. The resultant curve is given in Figure 2.

RELATIVE DAILY PHOTOSYNTHESIS IN THE OCEAN AS A FUNCTION OF LIGHT INTENSITY

If one knows the incident radiation falling on the surface of the ocean throughout the day and the extinction coefficient (k) of the water, it is possible to calculate from this information and the data in Figure 2 the daily relative photosynthetic rate at any depth in a water column in which the phytoplankton is distributed homogeneously.

A continuous record of incident radiation as measured by a 50-junction Epply pyrheliometer is kept by the Epply Laboratories of Newport, Rhode Island and was made available to the author through the kindness of Mr. Hedley Greer of that organization. According to Forsythe (1954) 50.4–52.3% of solar radiation falls within the range of 4000–7700 A, while according to List (1951) 42.5–45.25% falls within the range 4000–7000 Å. The present author has followed Edmondson (1955) in considering 50% of the total incident solar radiation as photosynthetically active.

Pyrheliometer values are expressed in energy units as gram calories per cm^2. These have been converted to units of luminosity using Jenkin's figures of 240 lumens per watt as suggested to her by Poole and Atkins, and results in the relationship 1 gram calorie per cm^2 per min (photosynthetically active radiation) = 15500 foot-candles.

The reflection of light from the surface of the water varies with cloud cover, surface roughness, and the altitude of the sun, but is normally rather small (Powell and Clarke 1936, Harvey 1955). For present considerations the light just penetrating the water has been taken as 95% of that incident to the surface. This is obviously an oversimplification and results in some overestimation of submarine light intensity, particularly in the early morning and late afternoon.

Figure 3 shows the light intensity in the surface layers of the ocean at the same latitude and under similar weather conditions which prevailed at Newport, Rhode Island, on June 17 and December 14, 1954, which were respectively the brightest and darkest days of the year. Mean intensities are given for half-hour intervals throughout

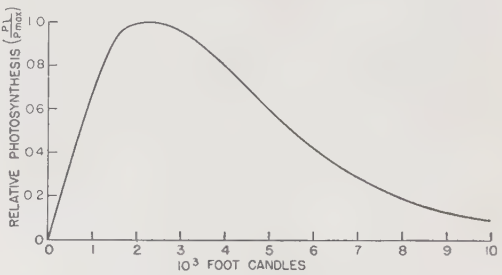

FIG. 2. Mean curve from Figure 1 showing relationship between photosynthesis and light intensity in marine phytoplankton.

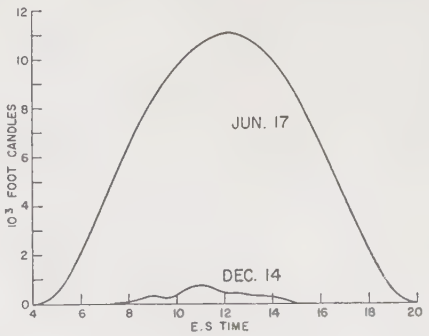

FIG. 3. Daily incident surface radiation at Newport, Rhode Island, on June 17 and December 14, 1954.

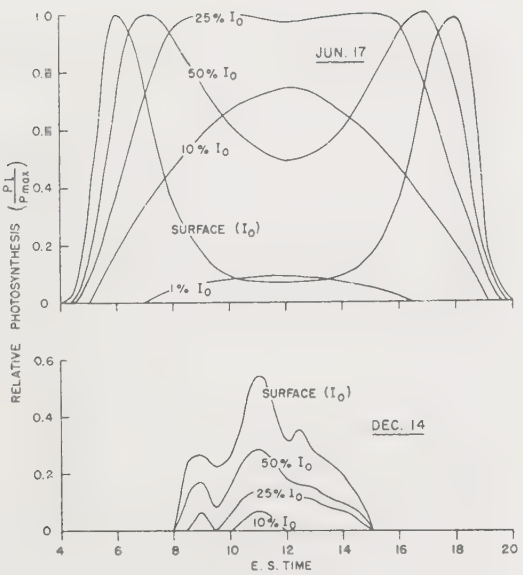

FIG. 4. Daily relative photosynthesis (P_t/P_{max}) at various depths in the ocean on June 17 and December 14, 1954, at a latitude and under weather conditions comparable to Newport, Rhode Island.

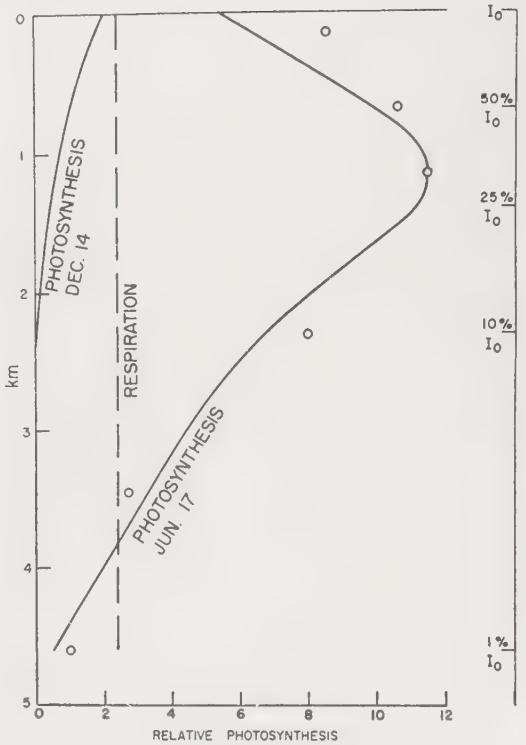

FIG. 5. Integrated daily relative photosynthesis (P_t/P_{max} × hrs. daylight/day) from surface to depth of penetration of 1% of surface light on June 17 and December 14, 1952. Dotted line represents respiration where $P:R$ at light saturation is 10:1 (see Text). Open circles from Steemann Nielsen (1952).

the day. Figure 4 shows relative photosynthesis also plotted at half-hour intervals at the surface and at the depths where the surface intensity is reduced to 50%, 25%, 10% and 1% of its initial value for the same two days, as obtained from Figures 2 and 3. Relative photosynthesis values may now be integrated over the entire day thereby giving daily relative photosynthesis at each depth considered (Fig. 5). The depth scale is given here as a function of the extinction coefficient of the water (km) as derived from the expression:

$$I_m = I_0 e^{-km}$$

where I_0 is the surface intensity and I_m the intensity at depth m. The curves in Figure 5 may, in turn, be integrated giving total daily relative photosynthesis within the entire euphotic zone.[2] These relative values, for the same value of k, are 29.2 and 1.8 for June 17 and December 14, respectively.

[2] Defined here as limited by the depth of penetration of 1% of the radiation incident to the surface. This is a constant depth (in water of the same transparency) but receives illumination which varies with the surface radiation. Thus the euphotic zone, as used here, has no biological significance other than defining the water mass below which no appreciable photosynthesis can occur.

A COMPARISON BETWEEN THEORETICAL AND MEASURED DAILY PHOTOSYNTHESIS CURVES IN THE OCEAN

In December, 1950, Steemann Nielsen measured C^{14} uptake in water collected from 10 meters and suspended at various depths in the Benguela Current of Luando, Angola, S. W. Africa (see Steemann Nielsen 1952: 129). The experiment was carried out on a bright, sunny day. According to Kimball (1928) the total daily radiation on a cloudless day at that time and latitude is 720 g.cal/cm². The length of the day was 12 hours and the altitude of the zenith sun 67°.

On June 17, 1954, at Newport, Rhode

Island, the total radiation was 802 g.cal/cm^2, the length of the day about 15 hours, and the sun's altitude also 67°. The two days were thus quite similar with respect to radiation, with the exception of the somewhat longer period of daylight at Newport.

Since Steemann Nielsen was dealing with a homogeneously distributed population (i.e. in using water collected from a single depth) it is possible to compare his curve of daily photosynthesis with the theoretical curve for June 17 at Newport. To do this, the depth scales must be equilibrated, which may be done by superimposing the points of maximum photosynthesis of the two curves. Thus maximum photosynthesis in the Benguela Current (at 10 meters) is arbitrarily assumed to occur where $km = 1.15$, k then becomes 0.115, and the remaining points may be plotted on Figure 5 using the same depth scale.

Photosynthesis is expressed in relative units. The rather good fit of Steemann Nielsen's data to the theoretical curve, considering that radiation in the two cases was not identical, lends some support to the preceding theoretical treatment and suggests that the response of the phytoplankton to light intensity was similar in the two cases.

THE RELATIONSHIP BETWEEN DAILY INCIDENT SURFACE RADIATION AND RELATIVE PHOTOSYNTHESIS WITHIN THE WATER COLUMN

In addition to the two days considered above (June 17 and December 14) the daily relative photosynthesis within the euphotic zone was calculated by the same method for 6 additional days in 1954. The 8 days chosen for this purpose were characterized by total incident radiation ranging at more-or-less even intervals from the darkest to the brightest day of the year. Relative photosynthesis was then plotted against total daily incident surface radiation for the 8 days (Fig. 6). The resulting smooth curve which may be drawn through the 8 points clearly indicates an empirically derived relationship between the two variables.

Records maintained at the Epply Laboratories include weekly averages of the total

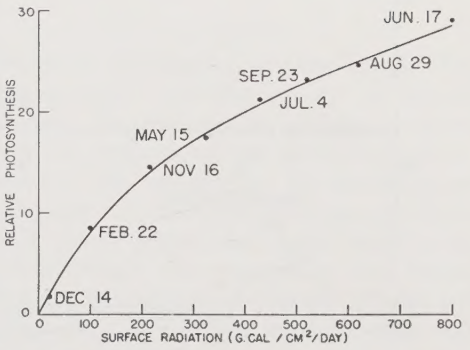

FIG. 6. The relation between total daily surface radiation and daily relative photosynthesis within the euphotic zone ($P_l/P_{max} \times$ hrs. daylight/day $\times k \times m$).

daily radiation at Newport, Rhode Island. These figures may be converted to photosynthesis values from the curve in Figure 6 to illustrate the effect of the seasonal variation of light intensity upon photosynthesis (Fig. 7). It should be emphasized here that this treatment considers only the factor of light and applies only to a hypothetical phytoplankton population which remains constant with respect to both time and depth within the euphotic zone. The actual magnitude of photosynthesis throughout the year varies as well with fluctuations in the population size, nutrient concentrations, and other limiting factors.

THE DETERMINATION OF ABSOLUTE PHOTOSYNTHESIS IN THE OCEAN

An absolute value for total photosynthesis (P), in mg of carbon assimilated per day beneath a square meter of sea surface, may now be obtained for a homogeneously distributed population from the expression:

$$P = \frac{R_s}{k} \times P_{sat}$$

where R_s = total relative photosynthesis within the euphotic zone for the appropriate value for total daily surface radiation (S), from Figure 6

k = extinction coefficient per meter, as measured

P_{sat} = measured total or "gross" photosynthesis at light satu-

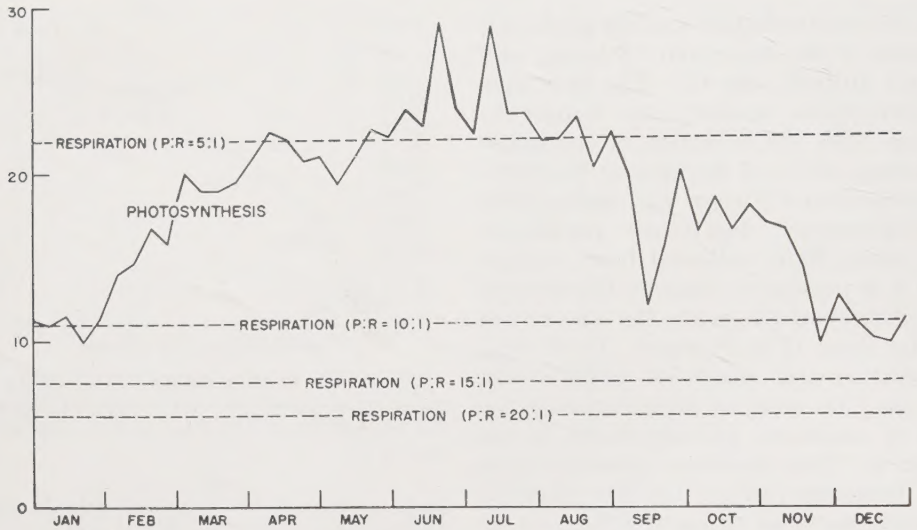

FIG. 7. Seasonal variation in daily relative photosynthesis and respiration within the euphotic zone. Different curves for respiration represent different ratios of $P:R$ at light saturation. Units as in Figure 6.

ration of a sample of the population, expressed as mg carbon/m^3/hour.

The value for (S) may be determined by measurement on the day in question, or may be taken from the published tables of Kimball (1928). The latter not only eliminates the necessity for measuring radiation, but also provides a mean value for the particular time and place under consideration. For purposes of a general survey of marine productivity, this is generally more significant than direct measurements on any single day, which cannot make allowance for the day-to-day variations in radiation resulting from local meteorological conditions.

The procedure outlined above may be used only under highly restricted conditions and is presented at this time merely to illustrate the ultimate applicability of the methods described herein. Procedures for estimating both total and net photosynthesis under varying natural conditions, based upon the same general approach as developed in this paper, will be described in a subsequent publication.

THE RATIO OF PHOTOSYNTHESIS TO RESPIRATION

At light saturation the ratio $P:R$ varies depending upon the state of nutrition of the algae. During exponential growth of *Dunaliella euchlora*[3] a maximum ratio of 12.1:1 was observed which decreased to about unity in cultures highly deficient in nitrogen and phosphorus (Ryther 1954). Kok (1952) found ratios in *Chlorella* as high as 20:1, but under "bad conditions" reported values as low as 1.4:1. In short term manometric measurements of photosynthesis, ratios of 20:1 or higher are commonly encountered, but the behavior of organisms under the highly artificial and idealized conditions of such experiments cannot be assumed to prevail over extended periods of growth.

It is not possible to measure the ratio directly in natural populations, since the respiration of the plants cannot be separated from that of the associated non-photosynthetic forms. At best it probably falls somewhat short of that observed under ideal conditions in laboratory experiments. Let us consider for the present a hypothetical situation in which the ratio of photosynthesis to respiration is 10:1 at light saturation. Respiration then assumes a value of 0.1 relative to maximum photosynthesis.

[3] Reported in that publication as *Chlamydomonas* sp. and correctly identified by Dr. Ralph Lewin.

Since respiration is essentially independent of light (Brown 1952) it remains constant throughout the day. Furthermore we are considering a population which is distributed homogeneously throughout the water column, so that R also remains constant with depth if we may disregard the effects of temperature. Except under conditions of extreme thermal stratification, which will be discussed below, temperature does not normally vary by more than a few degrees within the euphotic zone.

Daily respiration throughout the euphotic zone is then $0.1 \times 24 \times 4.6 = 11.04$ relative units, and this remains constant as long as the ratio $P:R$ at light saturation does not change. While absolute values for P and R are dependent upon the size of the population, their values relative to each other are independent of this factor.

In Figure 5, which shows the vertical distribution of daily relative photosynthesis within the euphotic zone on June 17 and December 14, the straight vertical line represents respiration. The point at which the curves for photosynthesis and respiration cross is the daily compensation depth. On June 17, this occurred at $3.83/k$ meters, which in clear oceanic water ($k \sim 0.04$) is about 95 meters and in coastal water ($k \sim 0.1$) is about 38 meters. On December 6 the curves never cross indicating that the plants could not compensate even at the surface. The daily ratio of $P:R$ for the euphotic zone was roughly 2.6:1 on June 17 and 0.2:1 on December 14, even though $P:R$ at light saturation was 10:1 in both cases.

In Figure 7, showing the seasonal pattern of photosynthesis, the horizontal lines represent respiration where $P:R$ at light saturation is respectively 5:1, 10:1, 15:1 and 20:1. This illustrates the fact that if a maximum ratio of 10:1 is reasonable, phytoplankton populations living at a latitude and under weather conditions comparable to Newport, Rhode Island, are unable to do more than compensate for their own respiration within the euphotic zone during the winter months. This, then, may account for the winter minimum of plankton algae in temperate and northern ocean waters.

DISCUSSION

We have discussed above the relationship between light and the ability of phytoplankton populations to maintain themselves or produce excess cellular material. Losses to the population by predation or sinking are not included in the scope of this report. Such permanent losses remove individuals from the population and hence affect the magnitude of photosynthesis and respiration, but not their relative rates with respect to each other.

For the purposes of this discussion the phytoplankton population must be considered to consist of those individuals which, through vertical mixing, spend at least some time in the euphotic zone. But the population, so defined, may extend considerably below the depth at which any photosynthesis can occur. In the open ocean this depth is of the order of 100–150 meters, in coastal waters 25–50 meters. The so-called "mixed layer" of surface water (i.e. water of the same density) may be and usually is considerably greater than these depths except in summer when thermal stratification occurs.

If one considers the entire population, as defined above, rather than that within an arbitrary depth, it is obvious that the $P:R$ ratio is even smaller than indicated above, at least during the late fall, winter and early spring when the mixed layer extends below the euphotic zone.

In summer the surface layers may be thermally stratified and mixing greatly reduced. Under these conditions the photosynthetically active population may not extend below the euphotic zone. But the reduction of mixing also prevents the homogeneous distribution of organisms in the upper layers and, due to the negative buoyancy of the cells, the population density increases with depth to a maximum somewhere below the depth of maximum photosynthesis (see Riley *et al* 1949: 73). This, too, will have the effect of increasing respiration relative to photosynthesis for the population as a whole. However, the effect here may be somewhat counteracted by the temperature gradient which results in lower respiratory rates near the bottom of the euphotic zone as compared

with that near the surface, whereas photosynthesis at the low light intensities found at these levels is essentially independent of temperature.

From these considerations it would appear that the $P:R$ ratio for the population may be considerably lower than indicated in the preceding calculations in which only the euphotic zone was considered. This leads to a reconsideration of the choice of a $P:R$ ratio at light saturation of 10:1. Since there are always some plankton algae in the surface layer of the ocean as well as animals which are dependent upon them for food, it would seem unlikely that there would be any extended period of the year in which no net photosynthesis can occur. Thus the $P:R$ ratio at light saturation is probably somewhat greater than 10:1. For reasons stated above, it is probably not consistently as great as 20:1, and a mean value probably lies somewhere between these limits. In Figure 7 the relative curve for annual respiration is shown where $P:R$ at light saturation is 15:1. If this curve is somewhat low for the entire population, as indicated above, the population would approach or reach compensation perhaps only in extreme conditions in mid-winter.

We have thus attributed the winter minimum of phytoplankton in temperate or northern latitudes to the limitation of light. In the normal course of events, this is followed by a spring maximum and a secondary fall peak interspersed by a mid-summer low. The latter has been attributed, at least in part, to nutrient depletion of the surface waters.

As soon as the limiting nutrient concentrations fall to the level at which exponential growth of the organisms can no longer occur at optimum light intensity, the rate of photosynthesis decreases and the ratio $P:R$ falls to 5:1 or less (Ryther 1954). Under these conditions photosynthesis by the entire population is able to compensate for its respiration only on days of the highest incident radiation, as is indicated in Figure 7. Thus light is always limiting to the photosynthesis of natural plankton populations and the effect of nutrient deficiency is at most additive to the light factor.

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